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Endless forms most wonderful: Four new cavernicolous planthopper species (Hemiptera, Fulgoromorpha, Cixiidae and Meenoplidae) from the Canary Islands

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Abstract
The Canary Islands harbour a rich and diverse fauna of obligate subterranean arthropods (i.e. troglobionts). Among the insect taxa which have repeatedly undergone the evolutionary switch from life on the surface to underground environments are the Fulgoromorpha, or planthoppers: Cixiidae and Meenoplidae. Previously, a total of 13 troglobitic planthopper species have been described from El Hierro, La Palma, Tenerife and Gran Canaria. Here we describe three new troglobitic cixiid species: *Cixius palmirandus* **sp. nov.** from La Palma, *Cixius theseus* **sp. nov.** from El Hierro and *Tachycixius gomerobscurus* **sp. nov.** from La Gomera, and one new meenoplid species: *Meenoplus skotinophilus* **sp. nov.** from El Hierro. *Tachycixius gomerobscurus* **sp. nov.** is the first record of a subterranean adapted Fulgoromorpha on La Gomera. With now 17 documented species of strictly hypogean planthoppers, the Canary Islands hold the highest number of subterranean planthoppers of any region worldwide, representing ca. ¼ of all known species. We provide a key to all subterranean planthopper species known from the Canary Islands as well as information on their habitat, distribution, ecological classification and conservation status. As all highly specialized, narrow range troglobitic planthopper species must be regarded as vulnerable, if not endangered,

climate change poses a major risk of extinction. We hypothesize on island colonization and subterranean speciation underlying taxonomic diversity and high endemicity. We conclude that the currently observed zoogeographic patterns imply the existence of an ancient fauna which is now extinct.

Keywords

Conservation, lava tubes, mesovoid shallow substratum, root feeders, subterranean adaptation, troglobionts, troglomorphy

Introduction

The Canary Islands are of purely volcanic origin, emerging the different islands from the sea level during the past 20.2 million years (Carracedo and Troll 2016). They are located in the Eastern Atlantic (27°37'–29°25'N, 13°20'–29°25'W), comparatively close to the adjacent continent: the most easterly island, Fuerteventura, lies just 100 km off the Northwest African coast. The seven main islands differ considerably in age (1.12–20.2 Ma), size (269–2034 km^2), and altitude (670–3714 m a.s.l.) (Machado 2022). Due to their geographical position in the Eastern Atlantic, the climate is essentially subtropical, although with considerable local variation in respect to precipitation and temperature. Distinct vegetational zones are recognized and range from arid and semi-arid scrub to humid laurel and pine forest and to subalpine areas on the higher central and western islands (Fernández-Palacios et al. 2001). Plants and animals which initially colonized the islands in many cases gave rise to radiations which have brought forth many endemic species: 41% of the ca. 1400 native vascular plant species and 45% of the ca. 7900 native terrestrial invertebrate species are endemic (Canarian Government [2024]). Less obvious, yet no less spectacular are geologic features: lava tubes and their unique species communities. Lava tube caves form in basaltic low-viscosity flows known as „pahoehoe" (Dutton 1884), or as ropy lava. They range in size from few centimeters in diameter to large tunnels of several meters high and decades of kilometers long (for formation of lava tubes see Peterson and Swanson 1974). Roots from the surface vegetation entering these hollow underground spaces provide a food resource for animals which inhabit the caves throughout their entire life cycle or parts of it (Howarth 1973).

The subterranean environment of the Canary Islands is rich in adapted arthopods – to date more than 230 troglobionts have been documented (e.g. Oromí 2004; 2008; Oromí et al. 2021). Yet it remains much less well investigated than surface biotopes, given the large number of lava tubes and existence of an extended mesovoid shallow substratum. Accordingly, in numerous taxa new species continue to be discovered with nearly any new survey, e.g., in the Curculionidae (*Oromia* Alonso-Zarazaga, 1987: García et al. 2020; *Baezia* Alonso-Zarazaga & García, 1999: García et al. 2021; *Laparocerus* Schoenherr, 1834: Machado 2022).

Insects frequently encountered in lava tubes on the Canary Islands are planthoppers of the families Cixiidae and Meenoplidae. While some do not differ in their external morphology from surface dwelling species of the taxon, and are likely occasional

visitors to the caves (trogloxenes), others display characteristic troglomorphies, such as reduction or loss of compound eyes, reduced and non-functional wings, and light bodily pigmentation, and are considered troglobionts (Sket 2008; Howarth and Moldovan 2018b), spending their entire life cycle in subterranean habitats.

Hitherto, a total of 13 subterranean adapted planthopper species belonging to the Cixiidae and the Meenoplidae have been described from El Hierro, La Palma, Tenerife and Gran Canaria islands (Remane and Hoch 1988; Hoch and Asche 1993; Hoch et al. 2012).

Recent biospeleological investigations in the western islands of the archipelago have revealed the existence of at least four previously unknown subterranean species, three in the Cixiidae, from La Palma, El Hierro and La Gomera, and one in the Meenoplidae, from El Hierro (see Fig. 1). The descriptions of these new species and providing information on their ecology and conservation status is the main objective of this article.

Outside the Canary Islands, strictly hypogean planthoppers are known from many parts of the world: from all continents except North America and Antarctica, and from several island archipelagoes – e.g., Hawaii, Galápagos, Samoa, Azores, Cape Verde (see Le Cesne et al. 2024; Bourgoin 2024).

Troglobitic planthoppers feed by sucking sap from roots (Howarth 1983; Hoch 1994), and it has been hypothesized that the utilization of roots as a novel food resource may have triggered the evolutionary switch from epigean to underground way of life (Howarth 1986). Within the subterranean communities, planthopper nymphs and adults are primary consumers, constituting prey for troglobitic scavengers and predators (Stone et al. 2005).

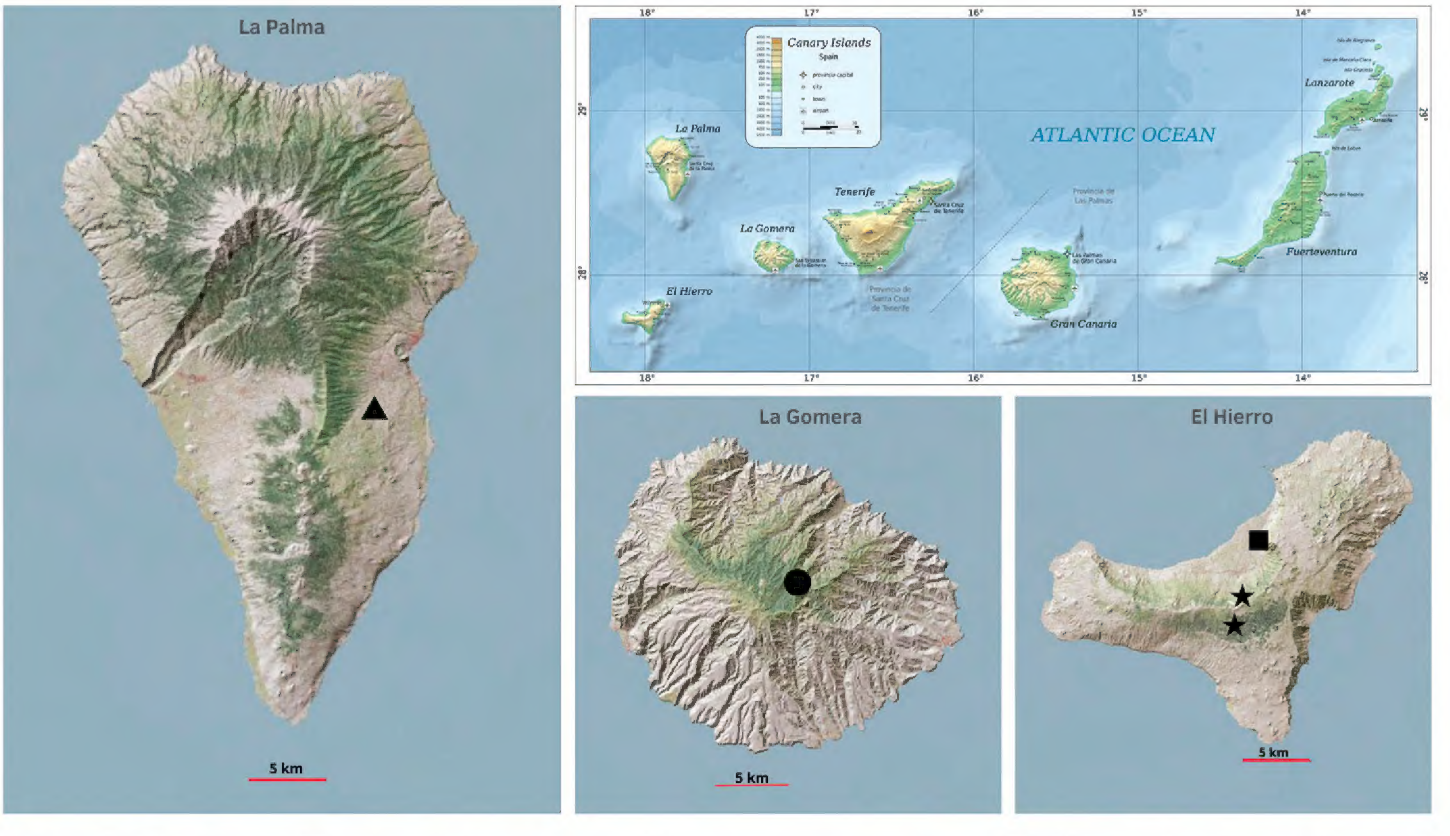

Figure 1. The Canary Islands and distribution of the new species described. Black triangle: *Cixius palmirandus* Hoch & Naranjo, sp. nov.; Black circle: *Tachycixius gomerobscurus* Hoch & Oromí, sp. nov.; Black stars: *Cixius theseus* Hoch & Aguín-Pombo, sp. nov.; Black square: *Meenoplus skotinophilus* Hoch & López, sp. nov. (https://commons.wikimedia.org/wiki/File:Map_of_the_Canary_Islands.svg; https://catalogo.idecanarias.es/geonetwork/srv/spa/catalog.search#/metadata/spagrafcan_MTLWMS_20160101).

Apart from living in lava tubes, these planthoppers have been documented from the „milieu souterrain superficiel“ (sensu Juberthie et al. 1980) or mesovoid shallow substratum (Culver and Pipan 2009) (henceforth referred to as MSS), which comprises a network of voids and cracks at the interface between soil and rock layer, and is characterized by similar conditions as those in deeper fissures or caves (Figs 2A–F, 3A–H).

Material and methods

Collecting, preservation, permanent storage

All the specimens used in this study were obtained in fieldwork carried out over many years in several islands of the Canary archipelago. Part of the studied specimens were collected inside lava tube caves by applying multiple sampling techniques (Wynne et al. 2019), mainly searching in those parts of the caves where roots appear abundantly, and then transferred immediately into vials containing absolute or 70% ethanol. Other specimens were collected using special permanent pitfall traps installed in the MSS (Fig. 3), according to López and Oromí (2010). For permanent storage, after dissection and examination, abdomen and genitalia were transferred to polyethylene vials containing glycerine, and individually associated with the specimen vial.

Morphological examination techniques, visualization

Measurements and examinations of external body features were made from the specimen in ethanol, without further manipulation. Measurements of body length refer to the distance between anterior margin of head and tip of anal segment in the male, and tip of ovipositor in the female. Terminology of wing venation follows Bourgoin et al. (2015). To prepare male genitalia for dissection, the genital capsule was removed from the specimen, macerated for 24h in 10% KOH at room temperature, washed in water, transferred to glycerine for storage, or to glycerine-jelly for drawings. Examinations and drawings were made using a Leitz stereomicroscope with *camera lucida* attachment.

Photographs

Habitus images of *Tachycixius gomerobscurus* sp. nov. (Fig. 8) were generated with a Leica Z16 microscope, with Planapo 2.0 X/WD 39 mm objective, with the aid of stacking software Helicon Focus 6.7.1. at the Museum für Naturkunde, Berlin.

Mitochondrial COI sequencing/barcoding

Non-destructive DNA extractions were performed for three individuals of *Meenoplus skotinophilus* Hoch and López sp. nov. to obtain their barcode sequences. The digestion of each voucher was done overnight at 60 °C with a pK buffer (ratio

Figure 2. Habitat types of hypogean cave planthoppers on the Canary Islands **A** Galería Honda de Miranda, La Palma (*Cixius palmirandus* sp. nov.) (Photo: Rafael García, used with permission) **B** Camino de San Salvador, MSS, El Hierro (*Cixius theseus* sp. nov.) (Photo: Pedro Oromí) **C, D** Reventón Oscuro, La Gomera (*Tachycixius gomerobscurus* sp. nov.), slope inside the laurel forest where the MSS traps (**D**, see also Fig. 3) are installed (Photos: P. Oromí (**C**); Salvador de La Cruz (**D**), used with permission) **E, F** Sima de Guinea, El Hierro (*Meenoplus skotinophilus* sp. nov.) **E** location **F** entrance (Photos: Miguel Ángel Rodríguez, used with permission).

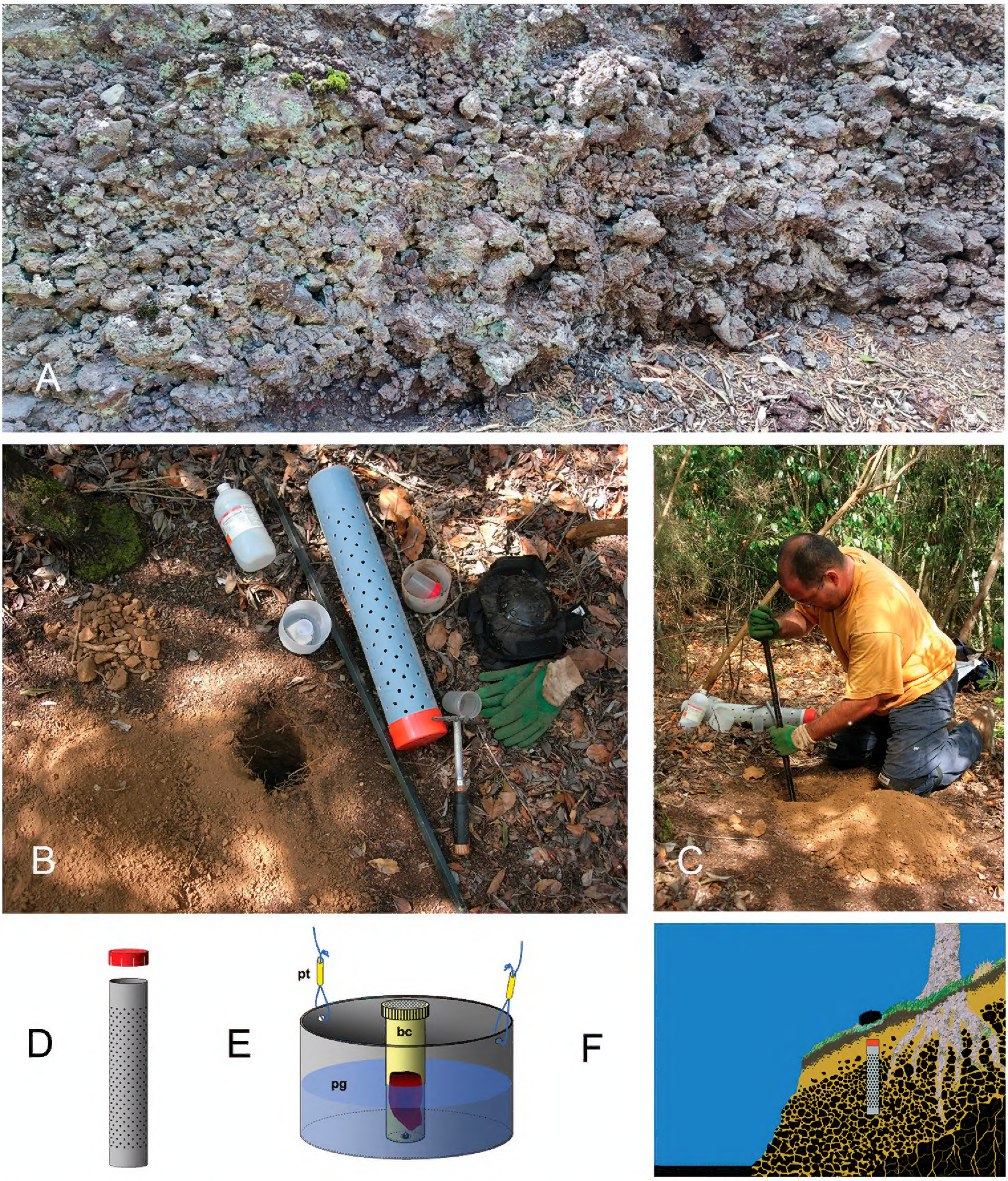

Figure 3. Collecting in the MSS **A** Detail of the MSS of El Hierro (Photo: Heriberto López) **B** Components of MSS trap and basic tools for installation **C** H. López installing a MSS trap in La Gomera island (Photos: Salvador de La Cruz, used with permission) **D** MSS trap: PVC pipe with multiple holes and silicone cover **E** sample collection container consisting of bait container (bc), nylon cords tied with small plastic tubes (pt) and tray with propylene glycol (pg) **F** trap installed in the MSS close to a road cut. **D, F** after López and Oromí (2010).

1/10). The supernatant (DNA lysate) was transferred to the corresponding well within a deep-well plate and the (DNA-extracted) vouchers were maintained in the vials with ethanol for further morphological studies. For the DNA extractions

of these specimens, we used the Mag- Bind Blood and Tissue DNA HDQ 96 kit (Omega Bio-Tek GA, USA) in the KingFisher robotic system (ThermoFisher Scientific inc.), and the Tecan Infinite 200 Pro (Configuration: Infinite M Nano+) to measure the DNA concentrations of the extracts. PCR amplification for the barcode region was done using degenerate Folmer barcode primers (Fol-degen-for: 'TCNACNAAYCAYAARRAYATYGG'; Fol-degen-rev: 'TANACYTCNGGRTGNCCRAA RAAYCA'; Folmer et al. (1994), Yu et al. (2012)). For PCR reaction, 2 μL of diluted (1/10) DNA extract was amplified with 23 μL of PCR mix (for a total volume of 25 μL), comprised of 14.4 μL of water, 2.5 μL of 10× NH4 buffer (Bioline), 1.5 μL of 50 mM MgCl2 (Bioline), 2 μL of 2.5 mM dNTPs (Bioline), 0.5 μL of BSA (20 mg/ml), 1 μL of each primer (10 μM), and 0.1 μL of Taq polymerase (BIOTAQ™ DNA Polymerase, Bioline). The PCR conditions were: initial denaturing step at 95 °C for 2 minutes, 40 amplification cycles (94 °C for 30 seconds, 46 °C for 35 seconds, 72 °C for 45 seconds), and a final step at 72 °C for 5 minutes. PCR success was checked by running products on a 1% TAE agarose gel, and successfully amplified products were cleaned following EXO I/rAP PCR cleanup protocol. The purified PCR product for each voucher was Sanger sequenced with ABI technology in Macrogen, Spain (https://dna.macrogen.com).

The obtained sequences were edited on Geneious Prime version 2020.0.3 (www.geneious.com), and then processed in BOLD (https://www.boldsystems.org) and Genbank (https://www.ncbi.nlm.nih.gov/genbank/) with the IDS tool using default setting parameters, to explore if *Meenoplus skotinophilus* sp. nov. has closely related species included in these databases of barcode reference sequences.

Depository

Specimens are deposited in the following collections:

DZUL	University of La Laguna, La Laguna, Tenerife, Canary Islands, Spain;
IPNA	Institute of Natural Products and Agrobiology (IPNA-CSIC), La Laguna, Tenerife, Canary Islands, Spain;
UMACI	University of Madeira Collection of Insects, Funchal, Madeira, Portugal.

Results

The three new species of Cixiidae described herein are *Cixius palmirandus* sp. nov. from La Palma, *Cixius theseus* sp. nov. from El Hierro and *Tachycixius gomerobscurus* sp. nov. from La Gomera; and the new Meenoplidae is *Meenoplus skotinophilus* sp. nov. from El Hierro (for distribution see Fig. 1; for a synopsis see Suppl. material 1: table S1). *Tachycixius gomerobscurus* sp. nov. is the first record of a hypogean planthopper from La Gomera.

Taxonomy

Cixiidae Spinola, 1839

Cixius palmirandus **Hoch & Naranjo, sp. nov.**
https://zoobank.org/95A7D931-15AE-4D57-ACA2-DB8969D0E9FD
Figs 4, 5A–F

Material examined. ***Holotype:*** Spain • male; Canary Islands, La Palma, Cueva Honda de Miranda; 28.63744940, -17.78849367; 17 Oct. 2015; M. Naranjo leg. (50353 **DZUL**).

Diagnosis. *Cixius palmirandus* is similar to the other cavernicolous *Cixius* species from La Palma, *C. palmeros* Hoch & Asche, 1993 and *C. pinarcoladus* Hoch & Asche, 1993 in habitus (degree of troglomorphy), body size, general configuration of the male genital morphology, but differs in several characters: upper portion of frons smooth (vs. pustulate as in *C. palmeros* and *C. pinarcoladus*), mesonotum with lateral carinae attaining posterior margin (unlike in *C. palmeros*), tegmen with Y-vein (Pcu, A1, Pcu + A1) complete (vs Y-vein incomplete in *C. palmeros* and *C. pinarcoladus*), genital styles with expanded distal portion highly elongate (vs spoon-shaped in *C. palmeros* and *C. pinarcoladus*), and aedeagus shaft ventrally with an obtuse ridge which is apically rounded, concave and distinctly curved ventrally (vs apically with an obtuse tip, as in *C. palmeros*, or directed straight caudally, as in *C. pinarcoladus*).

Description. ***Habitus***. Strongly troglomorphic with compound eyes absent, tegmina, wings and bodily pigmentation strongly reduced.

Body length. Male 3.9 mm (n = 1)

Colouration. Head, thorax and abdomen stramineous/yellowish, lateral carinae of head and lateral carinae of pronotum in anterior portion slightly darker. Antennae and legs whitish, tegmina translucent with costal vein yellowish, other veins unpigmented.

Head. Vertex short and wide, not separated from frons by a transverse carina, i.e., frons continuously rounded into vertex. Vertex laterally near posterior margin of head with two shallowly concave areas. Frons convex, in ventral view ca. twice as wide as medially long, smooth, without median carina, lateral carinae strongly ridged, directed laterally. Frontoclypeal suture highly vaulted. Post- und anteclypeus smooth, without median carina. Post- and anteclypeus together ca. 2.8 × longer than frons medially. Rostrum elongate, well surpassing hind coxae, 2^{nd} joint longer than 3^{rd}. Compound eyes and ocelli absent, the former position of the lateral ocelli faintly recognizable by a light roundish spot anteriorly of antennae. Antennae with scape very short, ring-like, pedicel globose, with sensory plaque organs feebly recognizable; antennae shielded anteriorly by lateral margins of frons.

Thorax. Pronotum short, ca. 4 × wider than medially long, and 1.5 × wider than maximum width of head; indistinctly tricarinate: median carina obtuse, lateral carinae distinct in anterior portion, diverging laterally, gradually vanishing; posterior margin of pronotum shallowly incised. Mesonotum slightly vaulted, ca. 1.3 × wider than medially long, in midline ca. 3 × the length of pronotum; tricarinate, with carinae obtuse

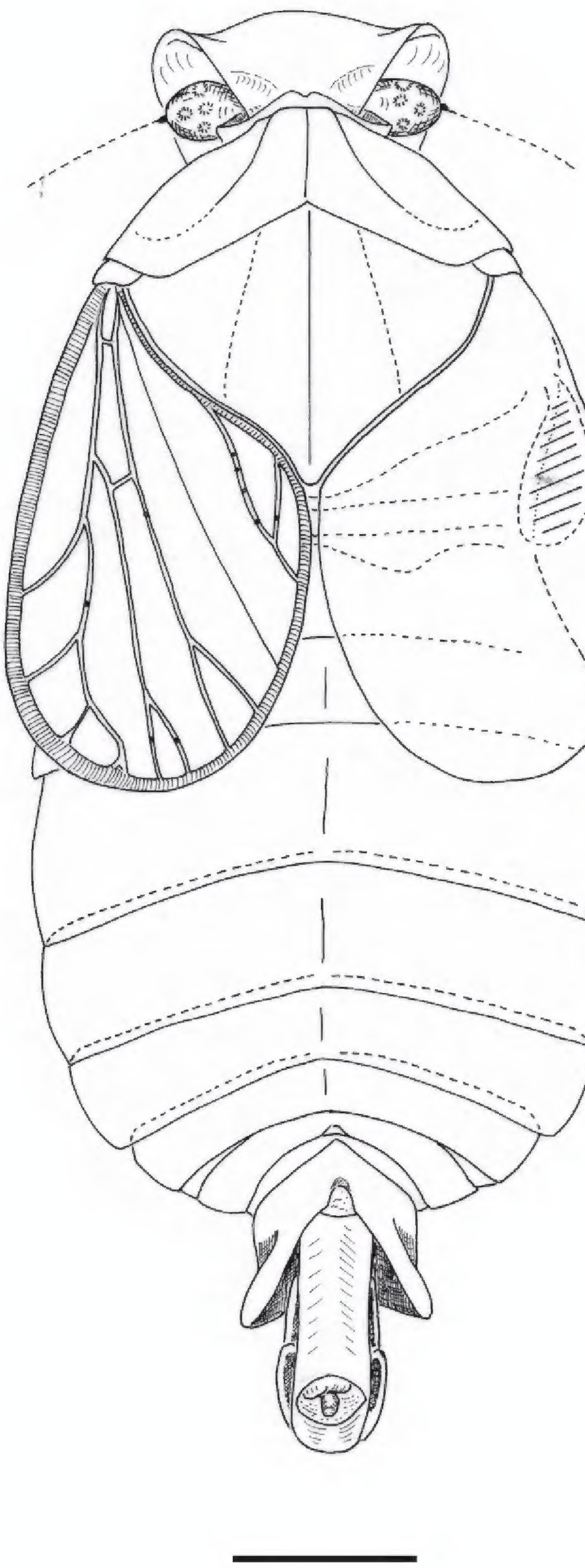

Figure 4. *Cixius palmirandus* Hoch & Naranjo, sp. nov. Habitus male (holotype). Scale bar: 0.5 mm.

and faintly recognizable, lateral carinae attaining posterior margin. Tegulae vestigial. Tegmina strongly reduced, venation as in Fig. 4. Costal vein in anterior and distal part of tegmen conspicuously wide; „Y-vein“ (Pcu, A1, Pcu + A1) preserved and recognizable. Tegmen ca. 1.6 × longer than maximally wide, attaining, respectively slightly surpassing posterior margin of third abdominal tergite. Longitudinal veins sparsely beset with bases of setae. Wings vestigial. Metatibiae laterally with 3 minute spines, distally with 6 teeth, grouped 5+1, lateral tooth longest. First and second metatarsal joints with 4 apical teeth, lateral ones longer than median ones. First metatarsal joint about as long as 2nd and 3rd joints together. Pretarsal claws slender, arolium small.

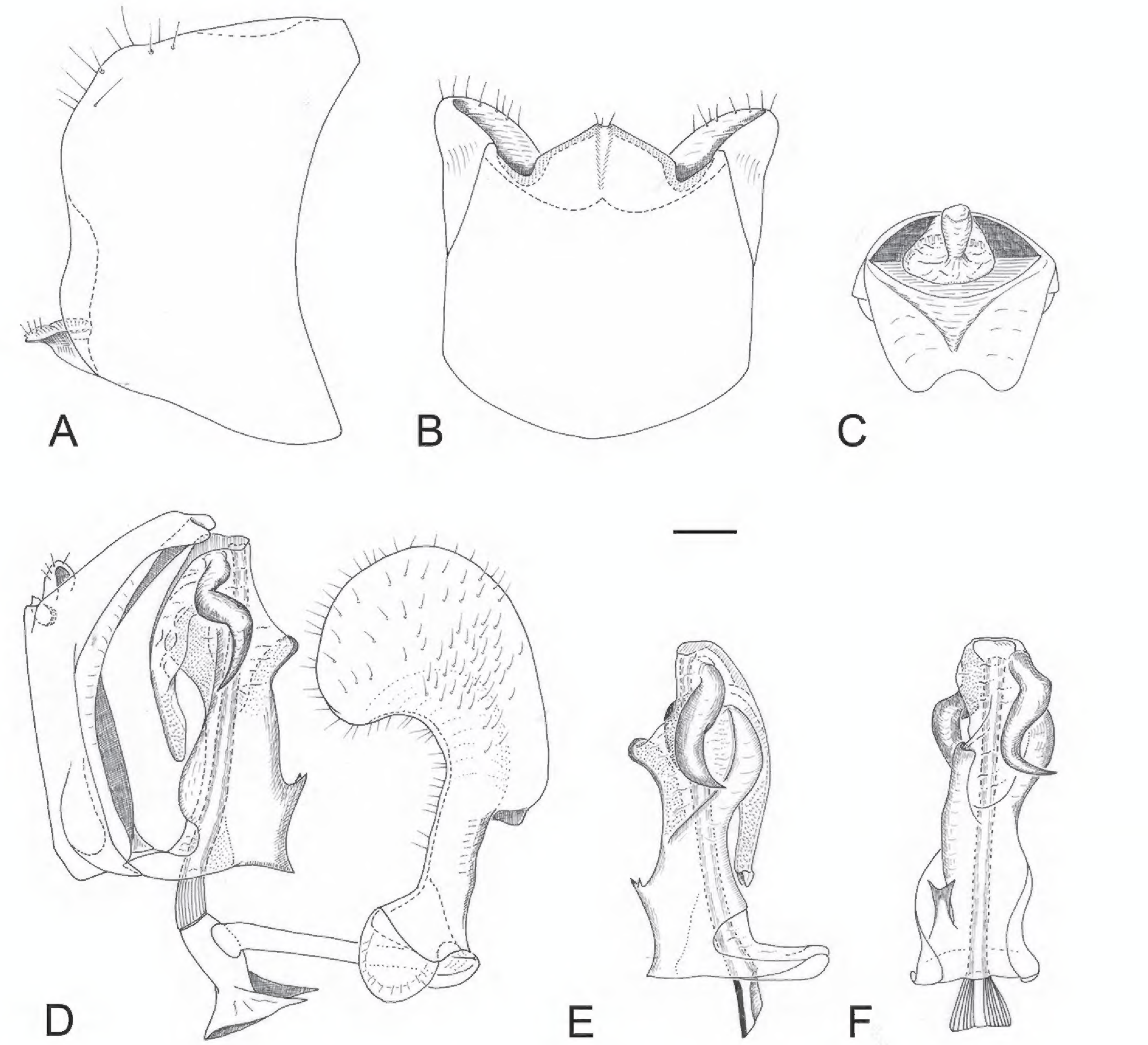

Figure 5. *Cixius palmirandus* Hoch & Naranjo, sp. nov. Male genitalia (holotype) **A** genital segment, right lateral aspect **B** same, ventral aspect **C** anal segment, caudal aspect **D** anal segment, aedeagus, genital style, *in situ*, left lateral aspect **E** aedeagus, right lateral aspect **F** same, ventral aspect. Scale bar: 0.1 mm.

***Male genitalia*.** Genital segment bilaterally symmetrical, in caudal aspect ca. 1.6 × higher than maximally wide, and in lateral aspect ca. 4 × longer ventrally than dorsally, caudal margins laterodorsally slightly expanding into rounded lobes, their margins beset with a cluster of long setae; medioventral process wide at base, distally tapering, tip in ventral view slightly incised, dorsal surface of medioventral process concave. Anal segment tongue-shaped, lateral margins straight, without ventral lobes, parallel from base to level of anal style, distally slightly tapering; anal segment distally of anal style bent ventrally in a ca. 45° angle, caudal margin produced into two short rounded lobes. Genital styles narrow in basal third, distally expanding, expanded portion elongate, distally rounded, medially concave; genital styles with dorsal margin of narrow portion and external surface of expanded portion densely beset with setae. Genital styles in repose joining in midline over nearly their whole length ventrally, nearly completely covering the aedeagus. Aedeagus with basal part (shaft) tubular, slender,

slightly compressed in basal two thirds, ventrally near base with two small rigid spines directed caudally; shaft ventrally with an obtuse longitudinal ridge which is apically rounded and in upper part slightly curved ventrally. Shaft subapically with a bulbous projection dorsally and right laterally, shaft apically with two sturdy movable spinose processes: left lateral one shallowly S-shaped, tip in repose directed basally, right lateral one slightly shorter than left lateral one, strongly curved and in repose directed right-lateroventrally, its tip pointing right laterally. Distal part of aedeagus (flagellum) in repose bent dorsally, narrow, surpassing midlength of shaft, but not attaining base of shaft; dorsally with a longitudinal ridge which is produced into a short, stout spine at apex, tip of flagellum directed right laterally.

Female. Unknown.

Etymology. The species epithet is an adjective in nominative singular, and a combination from the island of the type locality, La Palma, and the name of the cave, Cueva Honda de Miranda. The gender is masculine.

Distribution. Known from the type locality in the east of La Palma, municipality of Breña Alta (Fig. 1). Endemic to La Palma.

Ecology and behavior. Cueva Honda de Miranda is a lava tube located at 417 m a.s.l. in the eastern slope of the island. The potential vegetation in this area corresponds to a dry laurel forest (*Visneo mocanerae-Arbutus canariensis sigmetum*) (Del Arco and Rodríguez 2018). Currently, this space is occupied by agricultural plots and substitution scrub. The cave is a labyrinthic lava tube with over 20 galleries and 1 km of total development (Dumpiérrez et al 2000), in which seven troglobiont species have been recorded so far: the amphipod *Palmorchestia hypogaea* Stock & Martín, 1988, the isopod *Halophiloscia microphthalma* Taiti & López, 2008, the cockroach *Loboptera fortunata* Krauss, 1892, the thread-legged bug *Collartida tanausu* Ribes, Oromí & Ribes, 1998, and the beetles *Licinopsis angustula* Machado, 1987, *Domene benahoarensis* Oromí & Martín, 1990 and *Laparocerus dacilae* García, 1998. The gallery with the presence of *C. palmirandus* is located relatively close to the entrance to the cave, in which predominates a wide section, a high relative humidity and the presence of roots. The only specimen collected of *C. palmirandus* was dead but in good conditions for the formal descriptions of the new species. In this sector, an American cockroach nymph (*Periplaneta americana*) was observed, which may indicate local contamination by sewage.

Ecological classification. *Cixius palmirandus* sp. nov. displays several troglomorphic characters: absence of compound eyes and ocelli, strongly reduced tegmina and vestigial wings, and light body coloration. Although there is no information on the behaviour of the species, it is certainly unable to fly. The phenotypical configuration of eyes and wings suggests that it is restricted to the subterranean environment and likely to complete the entire life cycle underground. According to the criteria provided by Sket (2008), and more recently by Howarth and Moldovan (2018 a, b), we regard *C. palmirandus* sp. nov. as an obligate cavernicole, or troglobiont.

Conservation status. Cueva Honda de Miranda is located in an area of the island where the potential vegetation should be dry laurel forest (Del Arco and Delgado 2018), but it is currently heavily transformed into a rural environment dotted with scattered

homes and agricultural fields. The sewage sanitation system in the area is non-existent, and wastewater is generally discharged directly into underground wells, which are gradually contaminating the subsurface. Additionally, the chemicals used in the fields also accumulate in the subterranean environment over the years. Under these circumstances, the underground habitat loses its suitability for native subterranean species, as they are very sensitive to such habitat alterations. Furthermore, with this degradation, the underground habitat begins to be colonized by invasive species that thrive in these types of contaminated environments, competing with and displacing the native subterranean fauna. The detection of *Periplaneta americana* (Linné, 1758) in some areas of Cueva Honda de Miranda is a clear indication that its subterranean environment is likely undergoing such environmental degradation process. Nevertheless, there is no regular monitoring of the subterranean species populations present in the cave, which would provide precise information on whether they are experiencing some decline (Rafael García, personal comment). The sporadic sampling conducted so far in the cave has allowed for the capture of the only known specimen of *Cixius palmirandus* sp. nov., but the lack of continuity in these sampling efforts does not allow us to determine whether this species is scarce due to being rare, due to naturally low populations, or because they have indeed suffered a decline due to the deterioration of the subterranean environment. According to the IUCN criteria for assessing whether a species falls into one of the threat categories on its Red List, *Cixius palmirandus* meets criterion D2 (see IUCN 2022) due to its very restricted area of occupancy, which is less than 20 km^2, and the fact that it is known from only one location. Such circumstances make this species highly vulnerable to the impacts of human activities and stochastic events in a short time frame, potentially leading to its classification as Critically Endangered or even Extinct in the near future. Given these conditions, this new species should be classified as Vulnerable according to the IUCN criteria.

Remarks. The only known individual of this species, a male, was apparently collected and preserved in ethanol soon after the adult molt: the larval skin is still partially attached, and the cuticle still soft, thus the frons is distorted and the aristae of the antennae are missing. However, the male genital capsule appears to be fully sclerotized.

Cixius theseus Hoch & Aguín-Pombo, sp. nov.

https://zoobank.org/45F9D8C4-9242-4FC7-8B14-BFE941C28AB5
Figs 6 A, B, 7A–G

Material examined. ***Holotype:*** Spain • male; Canary Islands, El Hierro, Municipality of Frontera, Camino de San Salvador, MSS; 27.73294972, -18.01168166; 28 Aug. 2007; H. López and P. Oromí leg. (**IPNA**). ***Paratype:*** Spain • female; same data as holotype (50354 **DZUL**).

Additional material. Spain • 1 nymph III instar, 3 nymph IV instar; same data as holotype (**IPNA**).

Diagnosis. *Cixius theseus* sp. nov. is similar to the other cavernicolous *Cixius* species from El Hierro, *C. ariadne* Hoch & Asche, 1993 and *C. nycticolus* Hoch & Asche,

1993 in habitus (degree of troglomorphy), body size, general configuration of the male and female morphology, but differs in several characters: Frons 2.3 × wider than medially high and not pustulate (vs. 1.5 × wider and pustulate in *C. ariadne*); tegmen with Y-vein preserved (vs. reduced in *C. ariadne*); in the male genitalia: caudal margin of anal segment medially incised (vs. rounded in *C. ariadne*), genital styles with distal expanded part dorsally rounded (vs. dorsally produced in *C. ariadne*), basal part of aedeagus (shaft) left laterally with a prominent longitudinal ridge (vs. without such a ridge in *C. ariadne*), and with bifurcate ventral projection slender (vs. wide in *C. ariadne*), right lateral subapical spinose process sturdy and in repose curved dorsally (vs. slender and in repose curved basally in *C. ariadne*) and, most prominently, distal part of aedeagus (flagellum) with a slender spinose process at ca. midlength (vs. without such a spinose process in *C. ariadne*); in the female genitalia: caudal margin of 7th sternite medially expanding into an obtusely angulate process (as in *C. nycticolus*, vs. caudal margin straight in *C. ariadne*), and wax-secreting field on 9th tergite medially separated by a narrow, longitudinal, membranous area (vs. wax-secreting field medially not separated but with a distinct median ridge in *C. ariadne* and *C. nycticolus*).

Description. *Habitus*. Strongly troglomorphic with compound eyes absent, tegmina, wings and bodily pigmentation strongly reduced.

***Body length*.** Male 2.7 mm (n = 1). Female 3.3 mm (n = 1).

***Colouration*. Male.** Head and thorax incl. legs light yellowish, lateral carinae of head and posterior margin of vertex brownish; antennae whitish; tegmina translucent, whitish, venation white-yellowish, veins beset with brownish setae; legs whitish, distal spines of hind tibiae and of metatarsal joints brownish; abdomen whitish, genital capsule slightly darker, yellowish brown. **Female.** Head with vertex light yellowish, frons yellowish, medially with a brownish longitudinal stripe; clypeus light brown; antennae yellowish with distinct reddish brown star-shaped sensory plaque organs; pronotum medially, i.e., between lateral carinae, yellowish, lateral portions slightly darker, yellowish brown; mesonotum light yellowish; tegmina translucent, venation whitish, beset with brownish setae; legs yellowish white; abdomen light yellowish, genital segment incl. ovipositor yellowish brown.

***Head*.** Vertex short, ca. 3.5 × wider at base than medially long, very faintly separated from frons by an obsolete transverse carina. Frons convex, ca. 2.3 × wider than medially high, lateral carinae distinctly ridged and directed (antero-)laterally; frons smooth, without median carina, not pustulate. Frontoclypeal suture highly vaulted/arched. Post- and anteclypeus smooth, without median carina, together ca. 3.4 × longer than frons. Rostrum elongate, 2nd joint longest; rostrum relatively shorter in the male: surpassing caudal margin of hind coxae only slightly, in the female with ca. half the length of 3rd joint. Compound eyes and ocelli absent. Antennae with scape very short, ring-like, pedicel subcylindrical, ca. 1.4 × longer than wide, in the female with distinctly recognizable star-shaped sensory plaque organs.

***Thorax*.** Pronotum faintly tricarinate, lateral carinae diverging laterally, gradually vanishing; pronotum ca. 1.8 × wider than maximum width of head, and 4.2 × wider than medially long, posterior margin concave, obtusely angulate. Mesonotum

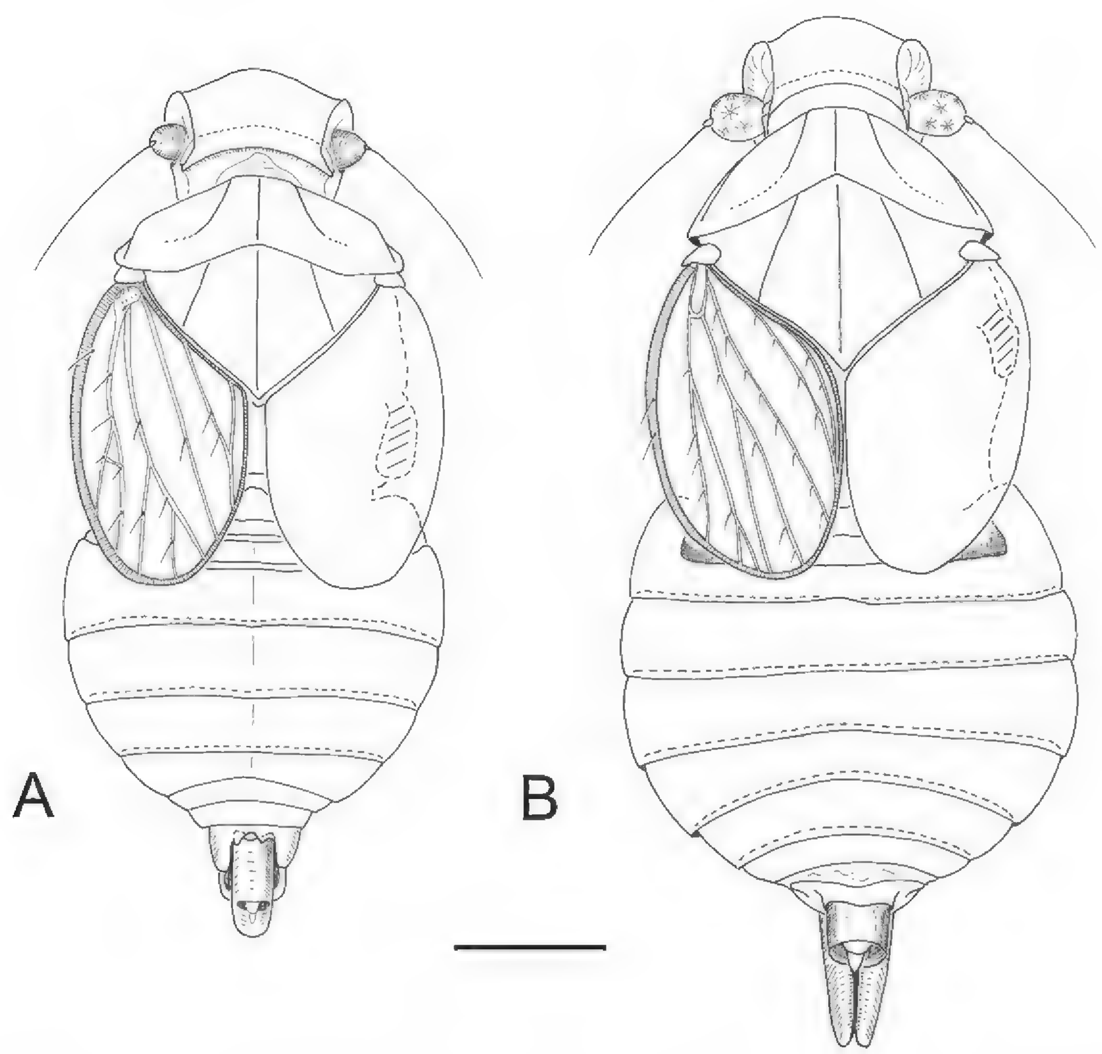

Figure 6. *Cixius theseus* Hoch & Aguín-Pombo, sp. nov. **A** habitus male (holotype) **B** habitus female (paratype). Scale bar: 0.5 mm.

tricarinate, carinae only faintly recognizable, lateral carinae reaching posterior margin, median carina feeble, obtuse, vanishing caudally; mesonotum in the male 1.5 ×, in the female 1.4 × wider than medially long, and in midline 2.3 × longer than length of pronotum. Tegulae small. Tegmina strongly reduced, their caudal margin attaining ca. midlength of 3rd abdominal tergite; tegmen longer than maximally wide: ca. 1.5 × in the male, and 1.65 × in the female; venation rudimentary, costal vein strong, basal cell closed, „Y-vein“ (Pcu, A1, Pcu + A1) preserved and recognizable, A1 and Pcu + A1 very close to posterior margin of tegmen; tegmina with numerous conspicuous setae along veins. Wings vestigial, very small.

Metatibiae laterally with 3 tiny spines, distally with 6 (in the male), and 6/7 (in the female) apical teeth, of which the lateral one is largest. First metatarsal joint in both sexes with 4, and second metatarsal joint with 4 (in the male) and ¾ (in the female) distal spines. First metatarsal joint about as long as 2nd and 3rd metatarsal joints together. Pretarsal claws slender, arolium small.

Male genitalia. Genital segment in caudal aspect slightly higher than wide, medioventral process simple, in ventral aspect obtusely angulate. Anal segment in dorsal aspect rectangular, ca. 2 × longer than wide, with distal portion slightly bent ventrally, lateral margins parallel, distal margin medially incised. Genital styles slender at base, distally expanding dorsally, expanded part medially concave. Aedeagus with basal part (shaft) slender, more or less tubular, left laterally with a prominent, longitudinal,

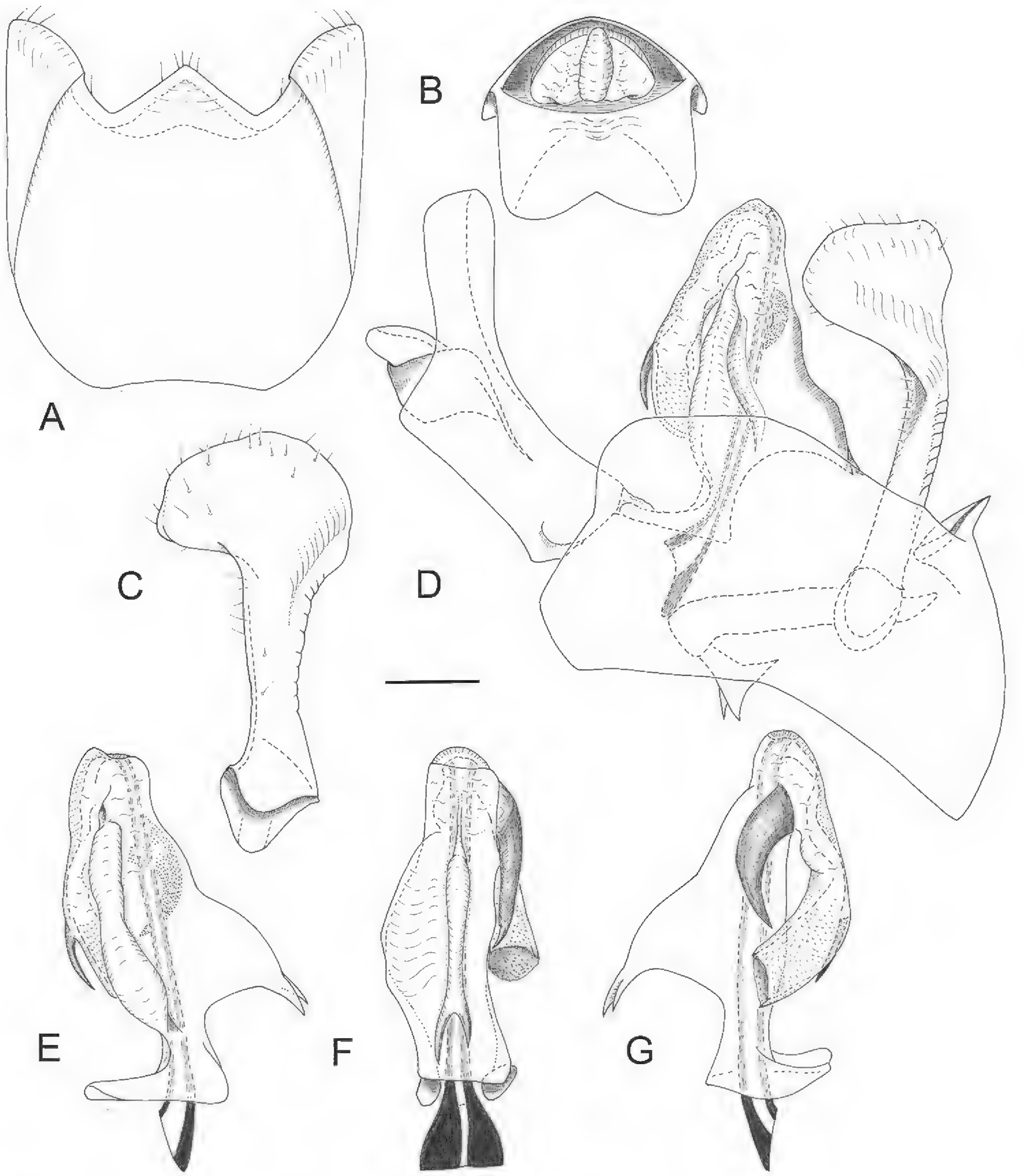

Figure 7. *Cixius theseus* Hoch & Aguín-Pombo, sp. nov. (holotype). Male genitalia **A** genital segment, ventral aspect **B** anal segment, caudal aspect **C** left genital style, maximum aspect **D** anal segment, genital segment, aedeagus and genital style, *in situ*, left lateral aspect **E** aedeagus, left lateral aspect **F** same, ventral aspect **G** same, right lateral aspect. Scale bar: 0.1 mm.

rounded ridge and ventrally with a bifurcate projection directed basally. Shaft subapically on its right side with a sturdy movable spinose process which in repose is curved basally, its tip pointing dorsally. Distal part of aedeagus (flagellum) tubular, in repose bent dorsally and to right side, surpassing midlength of shaft, with a slender, spinose process, in repose directed basally, left laterally at ca. midlength of flagellum; visible part of ejaculatory duct rugose; phallotreme wide, located apically.

Female genitalia. 7th sternite with anterior margin convex, highly vaulted cephally, rounded, caudal/posterior margin medially expanding caudally, expanded portion obtusely angulate. Ovipositor ensiform, slightly curved dorsally, caudally surpassing anal tube with less than 1/3 of its total length; anal segment tubular, short, in lateral view ca. 2 × higher than long, lateral margins more or less parallel; 9th tergite caudally truncate, wax-secreting field distinctly limited, slightly concave, medially separated by a narrow, longitudinal membranous portion.

Etymology. The species epithet is a noun in nominative singular and refers to Theseus, one of the heroes in Greek mythology, friend of Ariadne. The gender is masculine.

Distribution. Adults known only from the type locality (Camino San Salvador), in the laurel forest in the huge landslide of El Golfo, at the northwest of El Hierro (Fig. 1). Endemic to El Hierro.

Ecology and behaviour. El Hierro is the youngest island in the Canary archipelago, and the youth of the terrain is visibly apparent in much of its territory. Fields of recent lava abound, and a large part of the soil is made up of volcanic deposits where fine ash or more or less coarse lava clinker predominate, or a mixture of both in highly variable proportions. In the central, western, and northern parts of the island, it is very common to find terrains formed by a layer of lava clinker covered by fine ash or an already formed, thin edaphic soil. The scoria layer contains a dense network of interstices and cracks (Fig. 2, top right), well isolated from changes in humidity and temperature from the outside by the overlying fine pyroclasts or soil covering it. This type of MSS was described for the first time in El Hierro and named as "volcanic MSS" (Oromí et al. 1986). Under these circumstances, the layer of pyroclasts maintains a high humidity level and a rather constant temperature throughout the year, which allows for the establishment of fauna adapted to subterranean life. This configuration of volcanic deposits constitutes the most common type of MSS in El Hierro, extending across large areas of the island. In Camino de San Salvador, where *Cixius theseus* n.sp. was discovered, the MSS was exposed when the terrain was cut to build a road (Fig. 2B). The location is in the laurel forest whose dominant trees are *Morella faya* (Aiton) Wilbur and *Erica canariensis* Rivas-Mart., Osorio and Wildpret, and herbaceous plants in the vicinity of the traps are *Pericallis murrayi* (Bornm.) B. Nord. and *Urtica morifolia* Poir. The traps were set over the talus of the road crossing the laurel forest, at 1230 m a.s.l. Although a good representation of the entire troglobiont fauna present on the island has been collected in nearby areas using MSS traps, only the capture of this new cixiid species should be noted in Camino de San Salvador.

Ecological classification. *Cixius theseus* displays a high degree of troglomorphy: compound eyes and ocelli absent, tegmina strongly reduced, vestigial wings as well as light, almost white body coloration. This blind and flightless species is most likely restricted to subterranean environments throughout its entire life cycle. According to the criteria provided by Sket (2008) and Howarth and Moldovan (2018 a, b) we regard *Cixius theseus* as an obligate cavernicole, or troglobiont.

Conservation status. Although only a few individuals of *Cixius theseus* are known, this new species apparently would not have conservation problems for several reasons: i) the volcanic MSS is widely distributed throughout the northern slope of the island, so

habitat availability is not a limiting factor; ii) in general, this entire slope of the island with laurel forest is well-preserved and there are no houses that could be contaminating the subsurface with sewage; iii) since cixiids feed by sucking fluids from roots, the presence of laurel forest in high density across this area ensures a constant food supply. The initial results from the MSS traps in San Salvador showed very poor capture of troglobitic species, which led us to their deactivation soon, a reason why very few specimens of this new species are known. However, *Cixius theseus* also clearly meets criterion D2 as in the case of *Cixius palmirandus*, so it should be classified as Vulnerable according to the IUCN criteria.

Remarks. From the type locality, 4 unpigmented, eyeless cixiid nymphs (III. and IV. instar) were collected, which are here preliminarily identified as *C. theseus* sp. nov. (**IPNA**). Morphologically very similar nymphs have been recorded from another locality („Mercader, MSS4; 27 Jan. 2012; H. López leg.“ and „Mercader, MSS3; 18 Jun. 2012; P. Oromí and H. López leg.“), 1075 m a.s.l. (27.71294456, -18.02217521), on the southern slope of the island, 2.3 km far from San Salvador. Whether these are conspecific with *C. theseus* cannot be confirmed on the basis of morphological characters alone. It remains to be investigated whether *C. theseus* sp. nov. is more widely distributed on El Hierro.

Tachycixius gomerobscurus Hoch & Oromí, sp. nov.

https://zoobank.org/98930191-9075-4A0B-85F9-8799BEFD79C8
Figs 8 A, B, 9, 10A–G

Material examined. ***Holotype:*** Spain • male; Canary Islands, La Gomera, Reventón Oscuro, MSS T3; 28.12468504, -17.21638908; 2 Jan. 2012; P. Oromí leg. (50355 **DZUL**).

Paratypes: • Same data as holotype, except • 1 male, 1 female; 5 Feb. 2009; P. Oromí and H. López leg. (34924 **DZUL**) • 1 male (6962 **DZUL**), 2 males (7014 **DZUL**), 3 males (7074 **DZUL**); 30 Jun. 2009; P. Oromí and H. López leg. • 1 male; 1 Jul. 2009; P. Oromí and H. López leg. (34935 **DZUL**) • 2 males; T3; 4 Jan. 2010; P. Oromí leg. (7009 **DZUL**) • 1 female; 8 Jun. 2010; P. Oromí and H. López leg. (**UMACI**) • 1 male, 1 female; T1; 9 Jan. 2011; P. Oromí and H. López leg. (**UMACI**) • 1 male, 3 females; T1; 30 Jul. 2011; P. Oromí leg. (**IPNA**) • 1 male, 1 female; T3; 2 Jan. 2012; P. Oromí leg. (7038 **DZUL**) • 1 male, 1 female; T3; 26 Mar. 2015; P. Oromí leg. (**UMACI**) • 1 female; 17 Sep. 2015; P. Oromí leg. (**DZUL**) • 1 male; 31 Jul. 2024; P. Oromí leg. (**IPNA**: BC3166).

Additional material. • Same data as holotype, except • 3 nymphs V instar (6962 **DZUL**), 4 nymphs V instar; T1; 30 Jul. 2009; P. Oromí and H. López leg. (**UMACI**) • 3 nymphs V instar and 1 nymph IV instar; T3; 4 Jan. 2010; P. Oromí leg. (**UMACI**) • 1 nymph V instar and 1 nymph IV instar; T3; 8 Jul. 2010; P. Oromí and H. López leg. (**UMACI**) • 1 nymph V instar; 9 Jan. 2011; P. Oromí and H. López leg. (**UMACI**) • 1 nymph V instar; T1; 30 Jul. 2011; P. Oromí leg. (**IPNA**: BC2984) • 2 nymphs IV and V instar; T3; 2 Jan. 2012; P. Oromí leg. (**IPNA**: BC2982, BC2983) • 1 nymph V instar; T1; Jun. 2013; P. Oromí leg. (**UMACI**) • 2 nymphs III and IV instar; T1-4; 17 Nov. 2013; P. Oromí leg. (**IPNA**: BC2985, BC2986) • 1 nymph V instar; 17 Sep. 2015; P. Oromí leg. (**UMACI**) • 1 male; 31 Jul. 2024; P. Oromí leg. (**IPNA**: BC3165).

Figure 8. *Tachycixius gomerobscurus* Hoch & Oromí, sp. nov. **A** habitus male **B** head and thorax, dorsal aspect.

T1, T2, T3 are the different MSS traps set along ca. 100 m in the same location.

Diagnosis. In general appearance and in the overall configuration of male and female genital structures *Tachycixius gomerobscurus* sp. nov. ressembles *T. crypticus* and *T. retrusus* from Tenerife, but differs in the following characters: shape of vertex: vertex short, anterior margin very shallowly rounded (vs strongly convex towards frons in *T. crypticus* and *T. retrusus*); colouration of tegmina: less vividly coloured than in *T. crypticus* and *T. retrusus*; reduction of hind wings much stronger than in *T. crypticus* and *T. retrusus*; male genitalia: caudal margin of anal segment medially strongly concave (vs shallowly concave in *T. crypticus* and straight in *T. retrusus*); shaft of aedeagus with 3 subapical movable spines (vs. 2 such spines in *T. crypticus* and *T. retrusus*); female genitalia: 9th tergite medioventrally deeply incised, membranous excavation acutely triangular (vs 9th tergite medioventrally only shallowly incised, membranous excavation dorsally shallowly rounded in *T. crypticus* and *T. retrusus*); 9th tergite with wax-secreting field medially with a short, but distinct median ridge (vs without such a ridge in *T. crypticus* and *T. retrusus*).

Description. *Habitus*. In general appearance resembling *Tachycixius crypticus* Hoch & Asche, 1993 and *T. retrusus* Hoch & Asche, 1993 from Tenerife, although less vividly coloured; weakly troglomorphic (i.e. hypogeomorphic, see Deharveng and Bedos 2018): compound eyes present, but small, tegmina covering most of the abdomen but not attaining tip of anal tube in the male, respectively tip of ovipositor in the female; hind wings strongly reduced, vestigial.

***Body length*.** Male 3.8–4.05 mm (n = 4). Female 4.3–5.2 mm (n = 6).

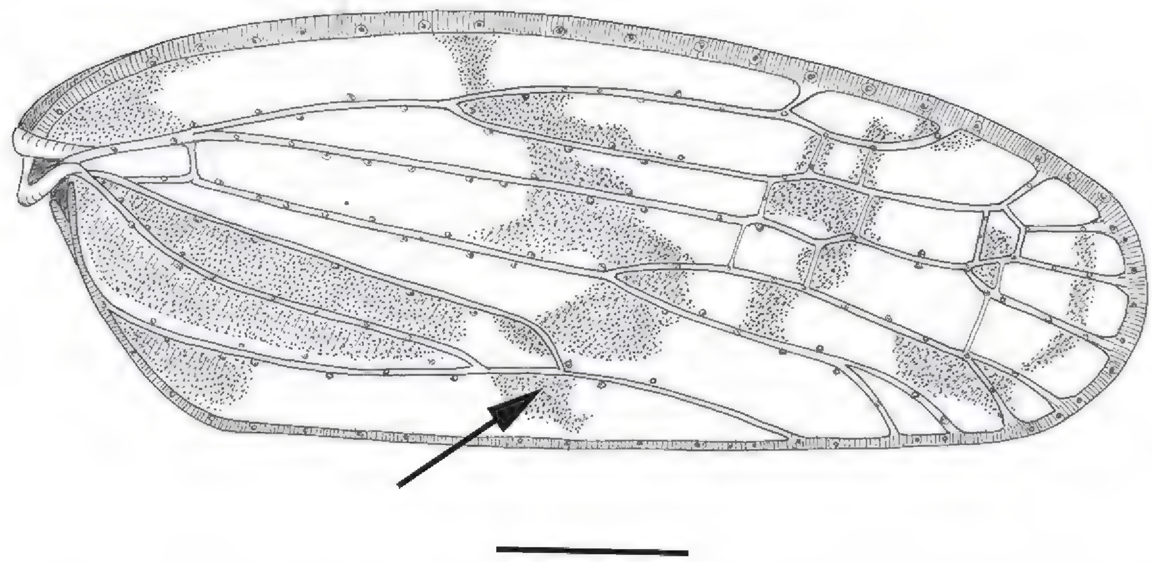

Figure 9. *Tachycixius gomerobscurus* Hoch & Oromí, sp. nov. Right tegmen (male). For meaning of arrow see text. Scale bar: 0.5 mm.

Colouration. Vertex, frons and head laterally light yellowish, with lateral carinae of vertex and frons and posterior margin of vertex slightly darker; antennae (pedicel) whitish; compound eyes reddish-dark brown; pro- and mesonotum light yellowish, otherwise thorax incl. Legs whitish, tips of lateral and distal spines of tibia, as well as distal spines of first and second metatarsal joints dark brown. Tegmina translucent, light yellowish, venation whitish, bases of setae along veins and margin of tegmen slightly darker, brownish; tegmen with anterior portion of triangle formed by cubitus posterior (CuP) and posterior margin of tegmen profusely brownish, and three irregularly limited, faint fuscous transverse bands: one at level of tegmen midlength, one at level of pterostigma, and one more or less parallel to distal margin (see remarks). Abdomen incl. genitalia light yellowish, or yellowish-brown, respectively.

Head. Vertex short, about 3.5 × wider at base than medially long, anteriorly rounded, with a faint median carina, areolets small, slightly concave, medially separated by an obtuse median carina; vertex indistinctly separated from frons by an obsolete transverse carina. Frons 1.2 × wider than medially high, with a distinct median carina, lateral carinae foliately produced laterally. Post- and anteclypeus with an obtuse median carina; together ca. 1.5 × longer than frons. Frontoclypeal suture strongly arched. Compound eyes present, compared to epigean *Tachycixius* species reduced in relative size, pigmented, lateral ocelli distinct, median frontal ocellus rudimentary. Rostrum elongate, well surpassing hind coxae, in males attaining anterior margin of 9th abdominal segment, in females attaining level of caudal margin of 9th tergite. Antennae with scape short, ring-like, and pedicel cylindrical, ca. 1.4 × longer than wide, with sensory plaque organs arranged in several rows.

Thorax. Pronotum tricarinate, lateral carinae ridged and diverging laterally near posterior margin of pronotum; pronotum short, medially ca. 1.8 × longer than vertex, and 1.7 × wider than maximum width of head (incl. compound eyes), posterior margin concave, medially forming an obtuse angle. Mesonotum tricarinate, carinae faint, lateral carinae attaining posterior margin of mesonotum; mesonotum 1.2 × wider than

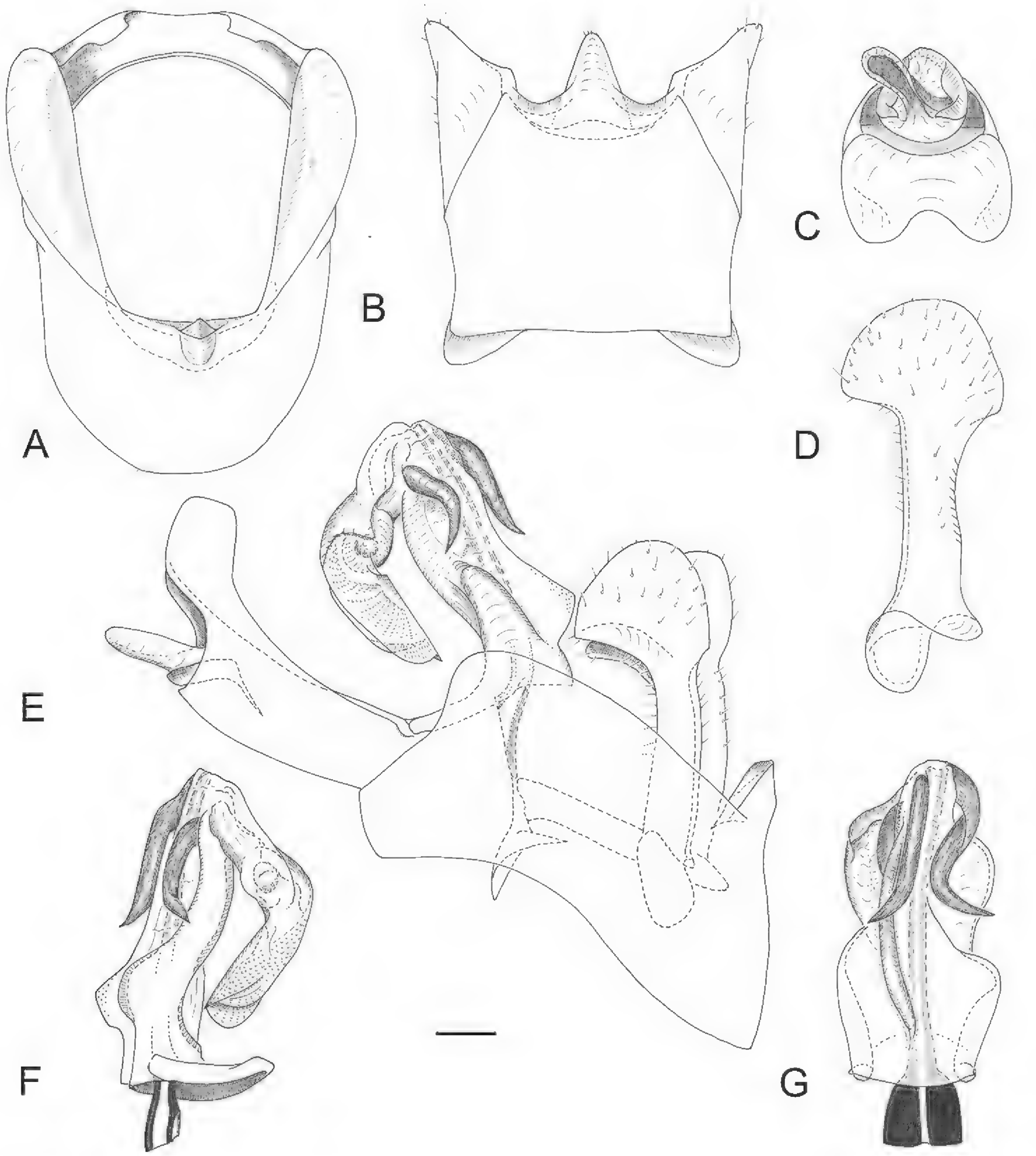

Figure 10. *Tachycixius gomerobscurus* Hoch & Oromí, sp. nov. Male genitalia **A** genital segment, caudal aspect **B** same, ventral aspect **C** anal segment, caudal aspect **D** left genital style, maximum aspect **E** anal segment, genital segment, aedeagus and genital styles, *in situ*, left lateral aspect **F** aedeagus, right lateral aspect **G** same, ventral aspect. Scale bar: 0.1 mm.

medially long, and medially 3.2 × longer than pronotum. Tegulae small. Tegmina distally reduced, in both sexes attaining caudal margin of anal segment, ca. 2.5 × longer than maximally wide; venation well developed, variable among specimens (in all specimens studied except for 1 female, the CuP vein does not connect to posterior margin of tegmen as is the case for most Cixiidae, but merges with PCu + A1 (= common stem of Y-vein, see Fig. 6, arrow), see remarks; basal cell closed, pterostigma faintly recog-

nizable; veins beset with or accompanied by numerous conspicuous bases of setae, on distal margin also between veins. Hind wings very small, vestigial, not surpassing posterior margin of metanotum. Metatibiae laterally in the majority of specimens studied with 3 small spines (variation: configurations 4/3 and 3/2 were observed in one female each), distally with 6 sturdy spines (in one female with 7 spines on one leg) (arranged in a row, lateral one strongest); metabasitarsus distally with 7–8 (bilaterally and individually variable), 2nd metatarsal joint distally with 7–8 spines (bilaterally and individually variable), each of the median 4 bearing one macroseta. Metabasitarsus slightly longer than 2nd and 3rd metatarsal joints together. Pretarsal claws short, stout, arolium small.

Male genitalia. Genital segment in caudal view ca. 1.3 × higher than wide, and in lateral view ventrally ca. 4.6 × longer than dorsally, caudal margins laterodorsally produced into 2 rounded lobes directed laterocaudally; medioventral process slender, triangular, dorsal surface with a faint median ridge. Anal segment elongate, narrow, in distal third bent ventrocaudally, in dorsal view ca. 2 × longer than wide at base, lateral margins in dorsal view more or less parallel, caudally of anal style converging, distal margin broadly rounded, ventral portion distally of anal style in caudal aspect strongly vaulted, with caudal margin medially concave; anal style elongate, slender. Genital styles narrow at base, distal third expanding dorsally, expanded portion caudally rounded, dorsally with an obtuse angle, medially concave. Aedeagus. Basal part of aedeagus (shaft) in proximal half wide, with three more or less compressed velum-like projections: one left laterally, extending from base to ca. midlength of shaft, one ventrally which is wide at base, narrowing at ca. midlength of shaft and extending from base almost to apex, and one right laterally which is broadly rounded and directed right laterocaudally. Shaft in distal half on right side with a compressed lobe extending right laterally, and subapically with 3 sturdy movable spinose processes: one left laterally, in repose curved dorsally, one ventrally, in repose directed basally, its tip pointing left laterally, and one right laterally, which is double-S-shaped, in repose curved basally and to right side. Distal portion of aedeagus (flagellum) well surpassing midlength of shaft, medially almost rectangularly bent and directed right laterally; without any spinose processes; distal portion of flagellum on ventral side expanding into a lobate, rounded protrusion, visible part of ejaculatory duct rugose, phallotreme wide, exposed dorsally.

Female genitalia. Seventh sternite subtriangular, anterior margin broadly rounded, caudal margin medially straight; ovipositor ensiform, slightly curved dorsally, caudally slightly surpassing anal segment; anal segment tubular, short, stout, dorsoventrally only slightly depressed; ninth tergite caudally truncate, wax-secreting field indistinctly limited, shallowly concave, with a short, but distinct median ridge; 9th tergite medioventrally deeply incised, membranous excavation acutely triangular, attaining dorsal third of 9th tergite.

Etymology. The species epithet is an adjective in nominative singular and a combination of Gomera and *oscuro*, the Spanish word for *dark*, probably used to create the toponym of this shadowy location inside the laurel forest. The gender is masculine.

Distribution. Known only from the type locality, Reventón Oscuro, municipality of Hermigua, in Garajonay National Park (Fig. 1). Endemic to La Gomera.

Ecology and behaviour. The MSS in Reventón Oscuro and in other places of Garajonay National Park is of the colluvial type, originated by accumulation of stone fragments at the base of rocky walls, and covered over time by soil (Juberthie et al. 1980, Mammola et al. 2016). The three traps set in Reventón Oscuro are on a steep slope inside a dense, humid and moderately dark laurel forest at 1035 m a.s.l. with a thin but rich organic soil covering the colluvium. All traps were set very close to tree trunks in order to protect them from gravitational collapse, and the colluvium was rich in small roots throughout its sampled depth (70–80 cm). La Gomera is the only island of the archipelago without lava tube caves due to the absence of volcanism in the last 2.5 Ma, but the MSS in the laurel forest is rich in troglobionts (Medina and Oromí 1990, Pipan et al. 2010, Gilgado et al. 2011, García et al. 2020). In this sense, Reventón Oscuro is the most diverse (13 species) among all Canary Island's MSS stations, as well as the most abundant in individuals (PO, HL unpublished data).

Ecological classification. *Tachycixius gomerobscurus* displays several troglomorphic characters, although not as strongly as *Tachycixius lavatubus* Remane & Hoch, 1988, *Cixius palmirandus* or *C. theseus*: the integument shows remnants of brownish pigmentation, the compound eyes are reduced in size, yet present, and ommatidia are pigmented; the lateral ocelli are distinct, the frontal ocellus is rudimentary. The tegmina are reduced distally, and hind wings are vestigial, much shorter than in the other MSS-dwelling species *T. crypticus* and *T. retrusus*. Although there are no observations on the behaviour of the species, we assume that individuals are unable to fly, but may be able to perceive visual input. As *T. gomerobscurus* has been collected from traps in the MSS, and given the presence of reduced but pigmented eyes, little is known about its behaviour. Despite its comparatively mild degree of troglomorphy, we assume that *T. gomerobscurus* is restricted to subterranean environments, and we therefore regard it preliminarily as an obligate hypogeomorphic troglobiont.

Conservation status. Over the past 15 years, nearly 40 individuals (both adults and nymphs) of this new species have been collected using MSS traps baited with liver or blue cheese. These individuals probably fell into the traps by chance rather than being attracted to the bait, as these planthoppers feed by sucking fluids from roots. The MSS site of Reventón Oscuro is the location in the Canary Islands where we have captured the largest number of troglobitic planthoppers using MSS traps, and the number of captures has remained relatively constant over the years. All evidence suggests that this species likely has a high density of individuals in this area. The region where this new species has been collected is a very well preserved national park, where a dense laurel forest ensures a consistent food supply in the subterranean habitat (roots). The limited known distribution of *T. gomerobscurus* on La Gomera is primarily due to the scarce sampling performed in the MSS at other sites on the island, being uncertain whether or not it has a broader distribution. However, although this species lives in a well-preserved habitat where it could apparently have a good population size, the IUCN recommends classifying it as Vulnerable according to criterion D2, since only one population is known distributed in a small area, which could completely disappear or enter a higher threat category if such a limited area were suddenly affected by impacts of human activities and/or stochastic events.

Remarks. The peculiar venation pattern observed in all but one specimens studied (the CuP merging with PCu + A1, i.e., the common stem of the „Y“ -vein instead of connecting to the posterior margin of tegmen) is very unusual not only for Cixiidae, but the Fulgoromorpha. It is likely a mutation in connection with the distal reduction of the tegmen, which has affected the overall venation pattern.

Some variation is observed in the colouration of body and tegmina: 2 specimens, 1 male and 1 female (coll. 2 Jan. 2012; T3) show very weak pigmentation of body and tegmina, and appear to have freshly molted into adult.

Meenoplidae Fieber, 1872

Meenoplus skotinophilus Hoch & López, sp. nov.

https://zoobank.org/7FA676EF-33CF-4D9C-A0DC-51C57D897EDE
Figs 11A, B, 12A, B, 13A–G,14A, B

Material examined. ***Holotype:*** Spain • male; Canary Islands, El Hierro, Cueva de Guinea; 27.77448369, -17.99866804; 22 Mar. 2021; H. López and C. Andújar leg. (**IPNA**). ***Paratypes:*** Spain • 2 males, 10 females; same data as holotype; (1♂ 50356 **DZUL**; 3♀ 50357, 50358, 50359 **DZUL**; 1♂7♀ **IPNA**).

Additional material. Spain • 14 nymphs IV instar, 5 nymphs V instar; same data as holotype; (16 nymphs **DZUL**; 3 nymphs (**IPNA**: BC1267, BC1268; BC1269)).

Diagnosis. *Meenoplus skotinophilus* is similar in general appearance and degree of troglomorphy to *Meenoplus claustrophilus* from La Palma, but differs from this species by the distally stronger reduced tegmina and lighter overall pigmentation. From the other two cavernicolous *Meenoplus* species on El Hierro (*M. cancavus* und *M. charon*), it differs distinctly by its degree of troglomorphy (compound eyes present, tegmina and wings well developed, tegmina surpassing tip of abdomen). While the general configuration of the male and female genitalia is similar in all four species (*M. claustrophilus*, *M. skotinophilus*, *M. cancavus* und *M. charon*), *Meenoplus skotinophilus* differs from these by the following characters of the male genitalia: ventrocaudal lobes of anal segment with median tips subacute and well separated (vs rounded and nearly apposed in the other species), aedeagus with apical margins of phallotreme angulate (vs rounded in the other species), and of the female genitalia: ventral valvulae distally with a beak-shaped, sturdy and acute tip pointing mediad (vs bearing a minute tip), and with proximal portion broadly lobate and finely serrate (vs rounded and smooth in the other species).

Description. ***Habitus***. Troglomorphies weakly defined except for compound eyes and pigmentation, tegmina and wings well developed, in repose surpassing the tip of the abdomen. In general appearance, intermediate between epigean Meenoplidae and strongly troglomorphic species, such as e.g., *Meenoplus cancavus* Remane & Hoch, 1988 and *M. charon* Hoch & Asche, 1993.

Body length. Male 2.8–2.9 mm (n = 3). Female 3.2–3.5 mm (n = 6).

Colouration. Head, pro- and mesonotum as well as male and female genitalia yellowish-brown, otherwise thorax und pregenital abdomen white. Compound eyes red. Teg-

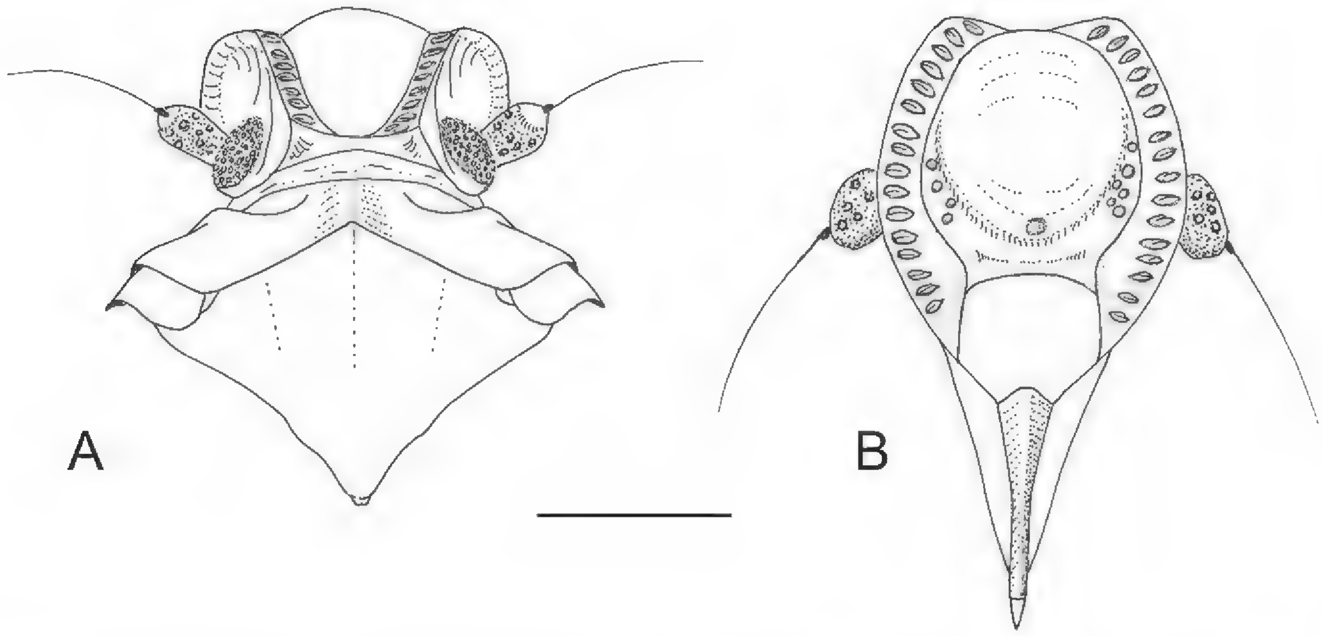

Figure 11. *Meenoplus skotinophilus* Hoch & López, sp. nov. **A** head and thorax, dorsal aspect **B** head, ventral aspect. Scale bar: 0.5 mm.

mina translucent, pale stramineous in males, light brown in females; venation as well as areas along veins and between sensory pits yellowish-brown. Wings hyaline, venation yellowish-brown. Legs stramineous, apical spines of tibia and tarsal joints I –II, light brown.

Head. Vertex very short, ca. 12 times wider than medially long, distinctly separated from frons by a ridged transverse carina. Frons strongly convex, anterior portion bulbous, about as wide as medially high, at and below level of antennae with a short row of small and hardly visible sensory pits irregular in number (4–6). Lateral carinae of frons foliately ridged and directed anterolaterad, anteriorly with a distinct row of large sensory pits; lateral lamelliform carinae continuing onto postclypeus. Frons smooth, without median carina, postclypeus shallowly, anteclypeus steeply vaulted. Compound eyes small, lateral ocelli vestigial, median frontal ocellus strongly reduced, ist former position marked by a light circular spot at the lower portion of the frontal bulbous area. Scape short, ring-like, pedicel cylindrical, ca. 1.7 times longer than wide.

Thorax. Pronotum medially about 3.5 times the length of vertex, posterior margin obtusely angulate; pronotum weakly tricarinate, median carina very feeble. Tegulae, tegmina and wings well developed; tegmina distally surpassing tip of abdomen with ca. 1/5 their total length. Tegmen with rows of sensory pits along the distal part of the costal vein, along ScP+R (+Ma), RP (+MA) and along PCu, A1, and their common stem PCu + A1 („Y-vein“). Metatibiae laterally unarmed, with 8 apical teeth. First metatarsal joint with 7 apical teeth, second metatarsal joint with 6 apical teeth.

Male genitalia. Genital segment in lateral aspect ventrally ca. 3 times as long as dorsally. Anal segment distally produced into two ventrocaudal lobes which converge medially, their median tips subacute and well separated from each other. Genital styles slender, narrow throughout, apically rounded, gently curved dorsad. Aedeagus tubular, stout, with phallotrema apically and dorsocaudally exposed, apical margins dorsally bluntly angulate.

Female genitalia. Strongly reduced, ventral valvifers produced into a rounded lobe; ventral valvulae with distal portion „bird-head-shaped“, i.e., caudally rounded

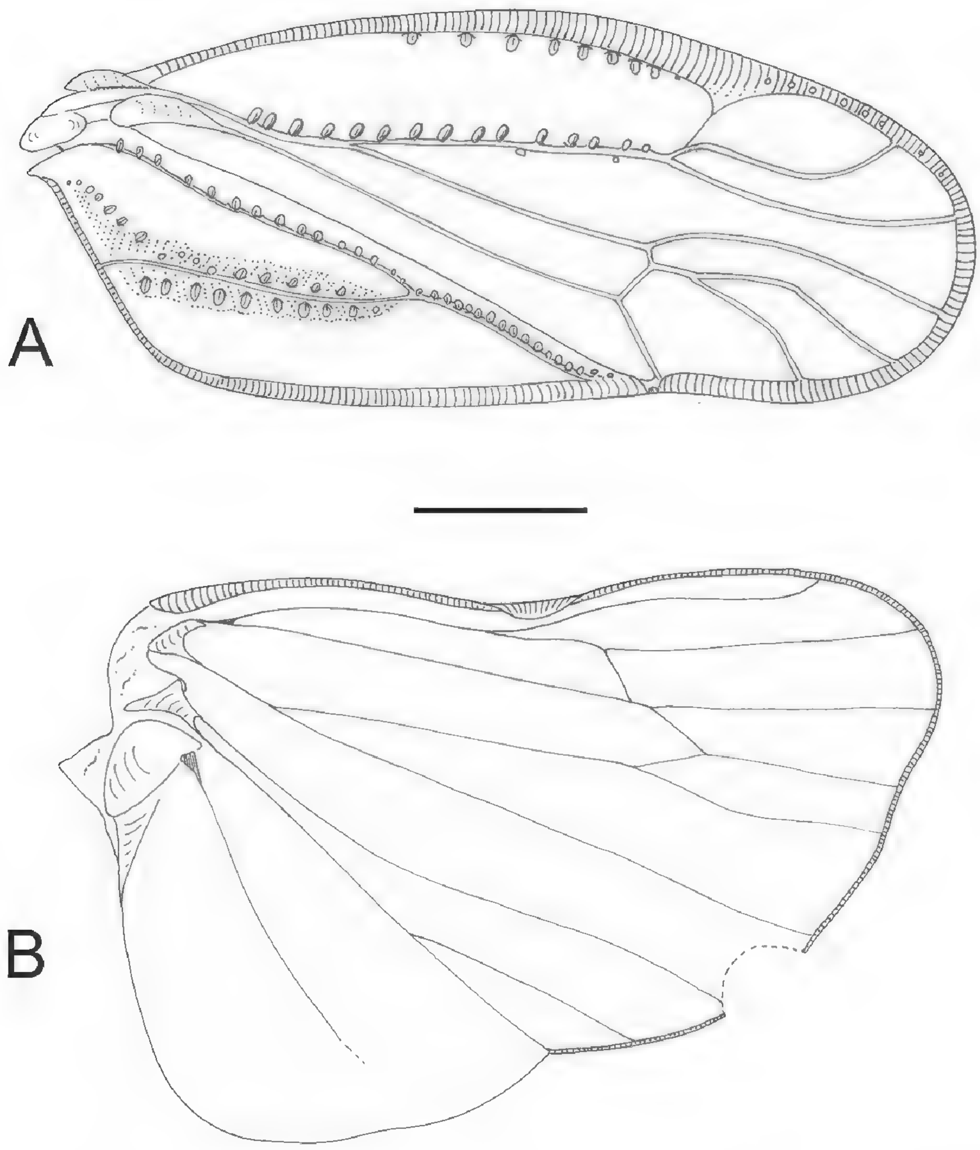

Figure 12. *Meenoplus skotinophilus* Hoch & López, sp. nov. **A** tegmen **B** wing. Scale bar: 0.5 mm.

and medially with an acute tip pointing mediad, and with proximal portion broadly lobate, with median margin straight and finely serrate, apposed.

***Molecular identification*.** Mitochondrial COI barcode sequences of 635 pb were obtained for three individuals of *Meenoplus skotinophilus* (specimen codes BC1267, BC1268 and BC1269). These individuals have identical barcode sequences, so no interpopulation genetic divergence has been detected. Either in BOLD or GenBank, no matches with similarity values greater than 85% were detected, so the genetic information that we supply is actually new for the genetic lineage of the group of species that may belong *Meenoplus skotinophilus*. The sequences were deposited in GenBank (accession numbers PQ530856, PQ530856 y PQ530856), with the following base composition:

AATGAGCCAGATTAATAGGTATAACAAGAAGAATAATTATTCGAATT-GAATTAATACAACCTGGTTCAATAATTAAAAATGATCAAATTTATA-ACTCAATTGTTACATCACATGCATTCATTATAATTTTTTTTTCAGT-TATACCCATCCTAATCGGTGGATTTGGAAATTGACTTGTACCTCTAAT-GATTGGAGCACCTGATATAGCATTCCCACGAATAAACAATATAAGCTTCT-GAATATTACCTCCATCACTAATACTATTAATTTTCAGTTCATTTTCAG-GTTCAGGTACAGGTACAGGATGAACAATTTATCCACCATTAT-

CAAGAATTCCTGCACATTCTGGCCCATCTACTGACTTATC-
TATCTTTTCCCTTCATATAGCAGGTGTAAGATCAATTCTAGGAG-
CAATTAATTTCATTTCAACTATTATTAATATACGACCTAAAATAATAA-
CAATAGAAAAAATACCCCTATTTTGCTGATCAATTTTCATTACAG-
CAATTTTACTTCTTCTATCATTACCTATTCTTGCAGGAGCAATTAC-
TATACTATTAACTGATCGAAACTTTAATACATCATTTTTTGATCCAACAG-
GAGGAGGAGACCCTATTTTATATCAACATTTATTT

Etymology. The species epithet is an adjective in nominative singular and a combination of the Greek words „skótos“ (= darkness) and „phílos“ (= friend). The gender is masculine.

Distribution. The species is kown only from the type locality, Cueva de Guinea, municipality of Frontera (Fig. 1). Endemic to El Hierro.

Ecology and behaviour. *Meenoplus skotinophilus* has been discovered in a lowland area of Frontera with a wide lava flow seemingly originating from the base of Tibataje cliff and extending towards the sea. The point from which the lava flow emerged is apparently clear, but no volcanic cone can be seen there, probably being buried under abundant sediment dragged from the cliff. In the upper part of the lava flow, close to the cliff, there is a complex of lava tubes, mostly unconnected but clearly formed during this eruption. One of them is Cueva de Guinea, a hardly 25 m long lava tube with a small entrance on the roof. At first the floor is rocky with scattered stones fallen from the ceiling, while in the last wider room clayish sediments cover the original substrate. The humidity is high and there are many roots attached to the walls and hanging from the ceiling. All this creates a good environment for the establishment of a community of invertebrates with some troglobitic species, like blind weevils and spiders, actually under study, besides a rich population of *Meenoplus skotinophilus* n. sp. around the roots. Also, American cockroaches (*Periplaneta americana*) were observed, both living specimens and remains. Outside the cave the vegetation is typical of dry areas and lava flows at low altitudes, where *Euphorbia lamarckii* Sweet, *Schizogyne sericeae* (L. f.) DC. and *Rumex lunaria* L. predominate.

Ecological classification. *Meenoplus skotinophilus* displays several troglomorphic characters, such as small compound eyes, reduced ocelli, and light, yellowish-white body coloration. Tegmina are reduced distally, but wings are well developed. Although there are no observations on the behaviour of the species, we assume that individuals may be able to perceive some visual input, and may have retained the ability of some, even if not sustained flight. According to the degree of troglomorphy, we assume that *Meenoplus skotinophilus* is restricted to subterranean environments, and we therefore regard it preliminarily as an obligate cavernicole or troglobiont, but of the hypogeomorphic type.

Conservation status. The area surrounding the cave entrance is part of an archaeological complex transformed into an open-air ecomuseum, which features reconstructed homes of the island's earliest inhabitants as well as those of later colonizers. The site also includes a center for the rehabilitation of an endangered endemic giant lizard and a natural cave that has been adapted for tourist visits. The volume of visitors is significant, and all facilities are equipped with bathrooms without connection to a sewage system, the wastewa-

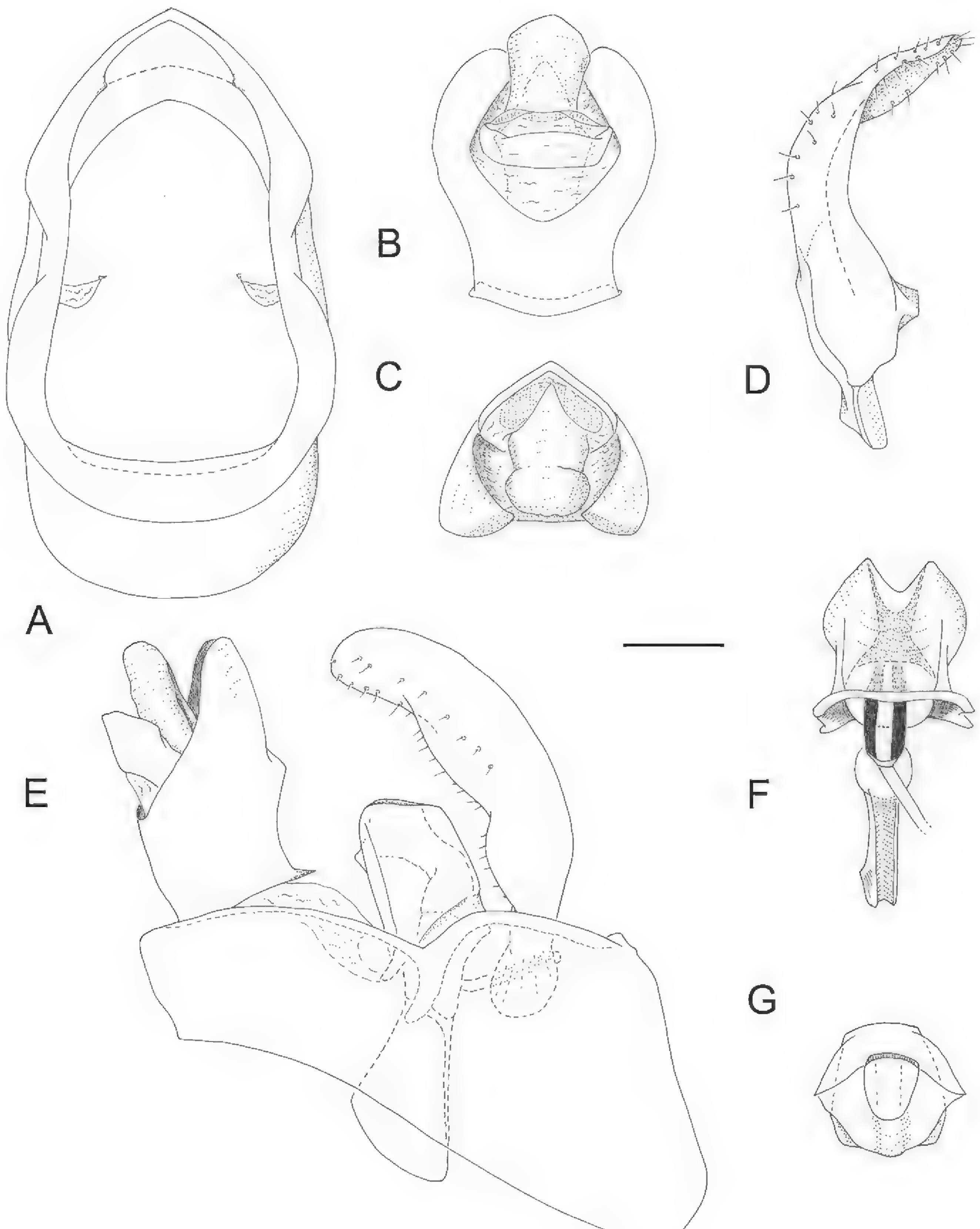

Figure 13. *Meenoplus skotinophilus* Hoch & López, sp. nov. Male genitalia **A** genital segment, caudal aspect **B** anal segment dorsal aspect **C** same, caudal aspect **D** left genital style, ventral aspect **E** anal segment, genital segment, aedeagus, genital style, *in situ*, left lateral aspect **F** aedeagus, ventral aspect **G** aedeagus, caudal aspect, view on phallotreme. Scale bar: 0.1 mm.

ter being discharged directly into underground wells. This practice gradually contaminates the underground environment, promoting the colonization of invasive species such as *Periplaneta americana* in both Cueva de Guinea and the nearby showcave. The deterioration of the subterranean environment poses a potential threat to native subterranean fauna, which

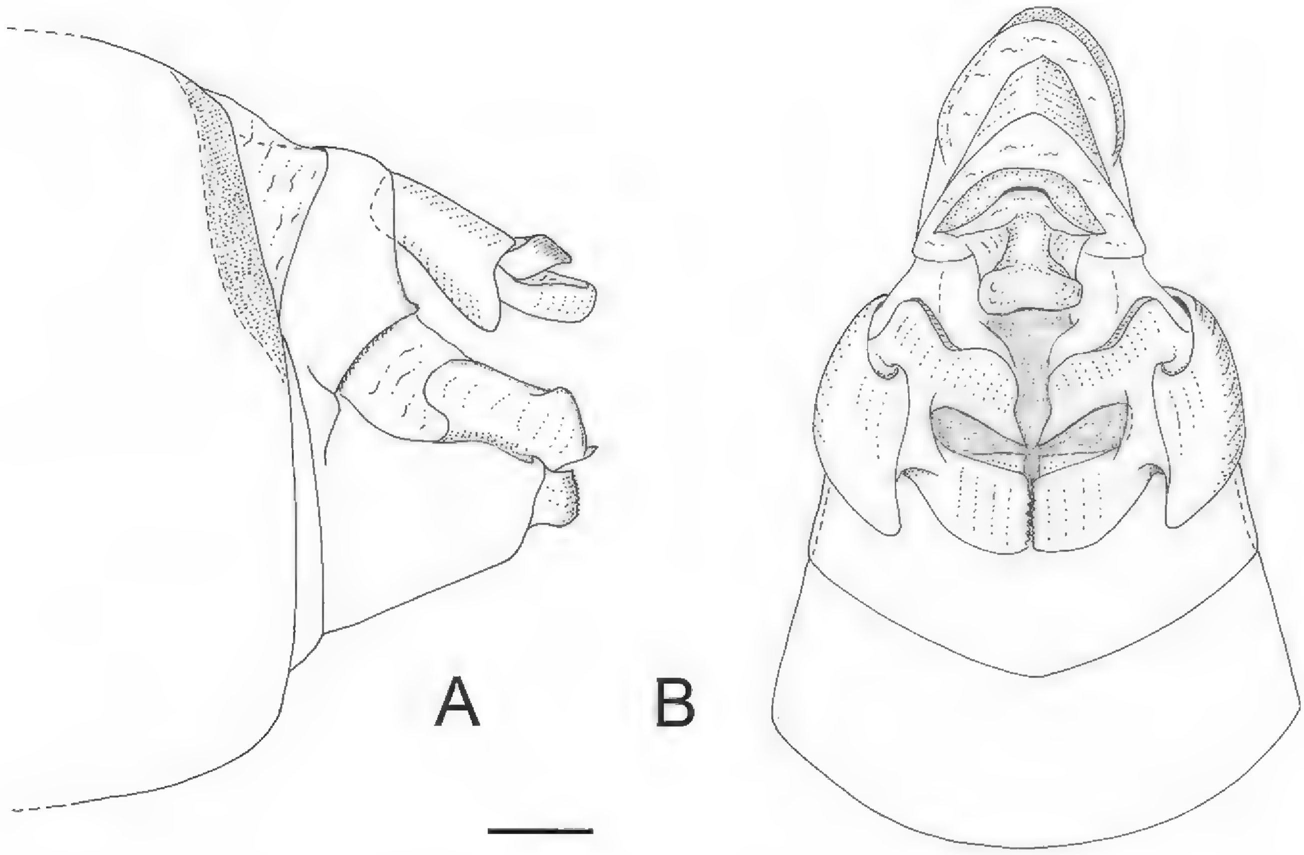

Figure 14. *Meenoplus skotinophilus* Hoch & López, sp. nov. Female genitalia **A** left lateral aspect **B** caudal aspect. Scale bar: 0.1 mm.

may either be displaced by invasive species or find their habitat unsuitable for survival. However, in the only sampling conducted in Cueva de Guinea *Meenoplus skotinophilus* was found abundantly, apparently with no serious threats at that time. To accurately apply the IUCN evaluation criteria to this species, it is essential to monitor its population in the short- to medium-term to determine whether it is indeed declining due to the aforementioned threats. However, M. *skotinophilus* should be included in the Vulnerable category based on IUCN criterion D2. In this case this is well justified given the intense tourist activity in the location where the only known population of this new species is found, being expected a strong negative pressure on its conservation in the short-medium term.

Remarks. Some nymphs of this new species have been selected for an ongoing genetic study with the aim of understanding the phylogenetic relationships between the three endemic species of *Meenoplus* present in El Hierro. This is a striking situation since it implies multiple speciation in the subterranean environment of a geologically very young island (1.12 Ma) in contrast to the absence of this genus on more mature islands rich in underground environments, such as Tenerife.

Key to the cavernicolous Fulgoromorpha species of the Canary Islands: adults of Cixiidae and Meenoplidae

The key is based on morphological characters of external structures and male genitalia, and geographic distribution. For species described here figure numbers are given in brackets, for species described by Remane and Hoch (1988), Hoch and Asche (1993)

and Hoch et al. (2012) compare figures in original descriptions. All species display troglomorphies in varying degrees, such as the reduction of compound eyes (small to absent), tegmina, wings, and bodily pigment, and occur in cryptic or subterranean habitats (lava tubes, MSS).

1 Head and tegmina without sensory pits: Cixiidae **2**

– Head laterally and tegmina with sensory pits: Meenoplidae **12**

2(1) Apical margin of forewing (tegmen) without tubercles between apical veins: *Cixius* Latreille, 1804 .... **3**

– Apical margin of forewing (tegmen) with tubercles also between apical veins: *Tachycixius* Wagner, 1939 .... **9**

3(2) *Cixius* species from La Palma. All species of very similar habitus (as in e.g., Fig. 4): strongly troglomorphic (absence of compound eyes and ocelli, light bodily coloration, and strongly reduced tegmina and wings), and similar configuration of the male genitalia: aedeagus shaft tubular, with 2 movable spinose process near apex, one right laterally and one left laterally; shaft ventrally near base with one or two short rigid spines directed towards apex; flagellum of aedeagus slender, apically with or without a spinose process; genital segment with medioventral process broadly triangular, apically slightly notched **4**

– *Cixius* species from El Hierro. All species with similar habitus, i.e. the degree of troglomorphy (see e.g., Fig. 6), and similar general configuration of male genitalia, e.g., medioventral process of genital segment broadly triangular, with blunt tip, anal segment elongate and distally bent ventrocaudally; shaft of aedeagus ventrally compressed, with a massive bifurcate projection directed basad, and right laterally with a single movable spinose process near apex. *Cixius nycticolus* Hoch & Asche, 1993 was described from 2 females and is thus not included in the key **8**

4(3) Flagellum of aedeagus with spinose process at apex **5**

– Flagellum of aedeagus without spinose process at apex................................ 7

5(4) Apical spinose processes of aedeagus shaft ventrally not exceeding midlength of shaft.. **6**

– Apical spinose processes of aedeagus shaft ventrally exceeding midlength of shaft, both processes in repose directed left laterally .... ***Cixius tacandus* Hoch & Asche, 1993**

6(5) Aedeagus shaft more or less tubular ... ***Cixius palmeros* Hoch & Asche, 1993**

– Aedeagus shaft ventrally distinctly compressed.. .... ***Cixius ratonicus* Hoch & Asche, 1993**

7(4) Aedeagus shaft tubular throughout, ventrally with two short spinose processes near base, the right lateral one of which is serrate .... ***Cixius pinarcoladus* Hoch & Asche, 1993**

– Aedeagus shaft with a distinct constriction at ca. midlength, ventrally with one rigid, apically bifurcate spine... ***Cixius palmirandus* sp. nov. (Figs 4, 5)**

8(3) Anal segment with distal margin rounded; aedeagus shaft with right lateral movable spine slender, in repose gently curved, directed basad, and bifurcate projection in ventral aspect with both spines equally long, left spine with an additional denticle near fork; flagellum of aedeagus not bearing any spinose processes .... ***Cixius ariadne*** **Hoch & Asche, 1993**

– Anal segment with distal margin medially shallowly incised; aedeagus shaft with right lateral movable spine sturdy, hook-shaped, with tip pointing basodorsally, and bifurcate projection in ventral aspect with left lateral spine longer than right lateral one, without any additional denticles; flagellum of aedeagus bearing a slender spinose process, arising slightly distad of midlength of flagellum and in repose directed basad ..... ***Cixius theseus*** **sp. nov. (Figs 6, 7)**

9(2) *Tachycixius* from La Gomera... ***Tachycixius gomerobscurus*** **sp. nov. (Figs 8–10)**

– *Tachycixius* from Tenerife **10**

10(9) Strongly troglomorphic: body whitish, compound eyes and ocelli absent; tegmina short, venation reduced, in dorsal aspect not covering pregenital abdomen, wings vestigial. Male genitalia with aedeagus shaft bearing three subapical movable spinose processes near apex, one arising left laterally, and two right laterally................ ***Tachycixius lavatubus*** **Remane & Hoch, 1988**

– Mildly troglomorphic: compound eyes present, small, tegmina longer than maximally wide, venation well developed, in dorsal aspect covering pregenital abdomen, wings reduced, ca. half the length of tegmina, body pale yellow with brownish portions, tegmina with brownish pigmentation pattern. Male genitalia with aedeagus shaft bearing two subapical movable spinose processes right laterally near apex **11**

11(10) Male genitalia: anal segment with ventrocaudal margin medially concave; genital style club-shaped, with caudal margin forming a blunt triangle; shaft of aedeagus subapically on its left side with a small membranous velum .... ***Tachycixius crypticus*** **Hoch & Asche, 1993**

– Male genitalia: anal segment with ventrocaudal margin straight; genital style spoon-shaped with caudal margin evenly rounded; shaft of aedeagus subapically on its left side with a small ear-shaped projection................................ .... ***Tachycixius retrusus*** **Hoch & Asche, 1993**

12(1) Troglomorphies weakly defined except for eyes and pigmentation; tegmina and hind wings well developed, tegmina in repose surpassing tip of abdomen, compound eyes present, but small... **13**

– Strongly troglomorphic: Compound eyes and ocelli missing, vertex and frons smooth, tegmina reaching but not surpassing tip of abdomen, venation reduced, wings vestigial... **14**

13(12) From La Palma .... ***Meenoplus claustrophilus*** **Hoch & Asche, 1993**

– From El Hierro .... ***Meenoplus skotinophilus*** **sp. nov. (Figs 11–14)**

14(12) From Gran Canaria........ ***Meenoplus roddenberryi*** **Hoch & Naranjo, 2012**

– From El Hierro **15**

15(14) Male genitalia with aedeagus in lateral aspect evenly rounded .... ***Meenoplus cancavus*** **Remane & Hoch, 1988**

– Male genitalia with aedeagus in lateral aspect apically almost truncate .... ***Meenoplus charon*** **Hoch & Asche, 1993**

Discussion

Taxonomic diversity, or why are there so many cave planthopper species on the Canary Islands?

So far, a total of 70 subterranean planthopper species from 6 families (Cixiidae, Meenoplidae, Kinnaridae, Delphacidae, Hypochthonellidae and Flatidae) have been documented worldwide (Bourgoin 2024; Le Cesne et al. 2024). With now 17 documented species of cave-adapted planthoppers, the Canary Islands hold the highest number of subterranean planthoppers of any region worldwide, representing ca. ¼ of all known species.

Their taxonomic and geographic distribution as well as putative epigean relatives is shown in Suppl. material 1: table S1. It is striking that the majority of species (12 out of 17) occur on the youngest islands, La Palma and El Hierro.

The primary habitat of troglobitic planthoppers is the deep cave zone where permanent darkness, stable temperatures and stable high relative humidity prevail (Howarth 1983), and where roots of surface vegetation penetrate the overlying rock and are abundant. Nymphs as well as adults rely on these roots for nutrition. The roots also serve as transmission channels for the species-specific vibrational signals which planthoppers produce in order to bring the sexes together for mating (see Hoch and Howarth 1993, and references therein). Lava tubes with intact and extended deep cave zones are rather short-lived, and usually do not persist longer than a few hundred thousand years (Howarth 1973). They form during the active lava flow phase and are colonized by pioneer plants on the surface soon after cooling of the newly formed rock (Howarth 1983). On El Hierro and La Palma with their maximum ages of 1.1 to 1.7 million years (Carracedo and Troll 2016) thus extended areas of suitable cave planthopper habitat exist, providing ample opportunities for cave-adaptation of epigean ancestral species.

On both islands volcanic activity prevails, and in La Palma the most recent eruption in 2021 along the Cumbre Vieja ridge not only created a new volcano, Tajogaite, but certainly many new lava tubes. Lava tube entrances in younger flows which have not yet developed a dense vegetation cover, however, are also easier to locate and access by researchers, hence a certain degree of collectors´ bias cannot be excluded.

Hoch and Asche (1993: 99) hypothesized „that in older and volcanically inactive islands .... progressive soil formation and erosion have presumably filled in the mesocaverns and dissected the cave passages causing much of the primary habitat of

rhizophagous troglobites to dissappear“. The subsequent discovery of *Meenoplus roddenberryi* in Gran Canaria in 2012, however, challenged this view. *Meenoplus roddenberryi* specimens were found in a small, 30 m long artificial water mine, at ca. 1100 m a.s.l, embedded in deposits of basaltic rocks of an estimated age of 3.7–2.8 Myr (Cueto et al. 1990). This indicates that troglobitic planthoppers may retreat into the interconnected cracks and crevices upon the decay of larger caves. It has occurred much the same in La Gomera where neither lava tube caves nor modern MSS of the volcanic type exist due to the lack of recent volcanism (Medina and Oromí 1990, Ancochea et al. 2006). But most of these ancient terrains had been covered by recent basaltic lavas at the time, with macrocaverns suitable for the presence of proper cave-dwelling planthoppers, probable ancestors of the current ones occurring in colluvial MSS. Anyway, given the high diversity of allopatric species in El Hierro and La Palma, it is expected that more new species might be discovered. In fact, we have knowledge of additional troglobitic planthoppers from Gran Canaria, Tenerife and La Palma, hitherto represented exclusively by nymphs and thus not identifiable to species level. We also have indications that the troglobiont cixiid species *T. lavatubus*, widespread on Tenerife, may constitute a complex of various cryptic species in the geologically young areas of the island (Hoch, Oromí, López, unpublished data).

Island colonization and cave adaptation

In the present-day epigean fauna of the Canary Islands the Cixiidae are represented by few taxa: *Cixius palmensis* Lindberg, 1960 endemic to La Palma; *Tachycixius canariensis* Lindberg, 1954 endemic to Tenerife and to be confirmed in Gran Canaria; *Hyalesthes* (with one widespread and several endemic species, Hoch and Remane 1985); and *Duilius seticulosus* (Lethierry, 1874) from Gran Canaria and Fuerteventura (Oromí et al. 2010; Bourgoin 2024). Of these genera, only *Cixius* and *Tachycixius* have given rise to species that permanently inhabit subterranean environments (Hoch and Asche 1993). Hitherto, no epigean Meenoplidae have been documented from any of the Canary Islands.

The distribution of cavernicolous planthopper species of the Canary Islands and potential epigean relatives is shown in Suppl. material 1: table S1.

Based on morphological information, we hypothesize that in the Cixiidae at least five to six, and maximally as much as 12 successful underground colonization events have taken place.

In the Cixiidae, the minimum number are: 3 on Tenerife (*Tachycixius lavatubus*; *T. crypticus*; *T. retrusus*), 1 on La Gomera (*Tachycixius gomerobscurus*), 1 on La Palma (*Cixius palmeros* + *C. pinarcoladus* + *C. ratonicus* + *C. tacandus* + *C. palmirandus*) and 1 on El Hierro (*C. ariadne* + *C. nycticolus* + *C. theseus*).

On Tenerife, *T. crypticus* and *T. retrusus* seem to have evolved after a common *T. canariensis*-like ancestor, but very probably represent two separate subterranean invasions, given that all troglobitic arthropods from the Anaga peninsula are always local endemisms allopatric to other hypogean species from the rest of the island; the highly

different geologic origin and age of Anaga have somehow isolated its subterranean environments and, consequently, promoted the formation of its own fauna (Oromí and Martín 1992). The morphological similarity between these three species suggests a closer relationship (Hoch and Asche 1993); however, without a DNA-based molecular phylogeny it is impossible to determine which scenario underlies the current situation.

Also, for the five cavernicolous *Cixius* species on La Palma which are morphologically similar to each other, it cannot be determined at this point whether they represent five separate cave invasions, or whether the differentation occurred subsequently to cave adaptation of a single species, which may or may not have been similar to *C. palmensis*, the only present-day epigean representative of the genus.

For the troglobitic *Cixius* species on El Hierro, *C. ariadne* and *C. theseus*, which are morphologically similar to each other, but clearly representing a lineage separate from the troglobitic *Cixius* species on La Palma, no epigean relative could yet be identified (*C. nycticolus* is not assessable due to the lack of information on male genital morphology). Also, for these two species it cannot be assessed on the basis of morphological information alone whether cave adaptation occurred once or twice.

In the Meenoplidae, the situation is even more puzzling. Albeit epigean species have not been reported from the Canary Islands, morphological information suggests that there must have been at least two lineages colonizing the Islands: one on Gran Canaria (ancestral to *Meenoplus roddenberryi* Hoch & Naranjo, 2012) and (at least) one on La Palma and El Hierro (ancestral to *Meenoplus claustrophilus*, *M. cancavus*, *M. charon* und *M. skotinophilus* which display high similarity in male genital characters). It is worth noting that these are the only three islands in the archipelago hosting *Collartida* (Hemiptera: Reduviidae) troglobionts, another genus without epigean representatives (Davranoglou et al. 2022).

For the cavernicolous Meenoplidae we assume 3–4 underground colonization events: one on Gran Canaria (*M. roddenberryi*), one on La Palma (*M. claustrophilus*), one or two on El Hierro (*M. cancavus*, *M. charon*, *M. skotinophilus*). It remains uncertain whether *M. cancavus* and *M. charon* are the result of separate cave invasion events, or whether speciation occurred subsequent to cave adaptation. Both species are strongly troglomorphic and differ considerably in external morphology from the less troglomorphic *M. skotinophilus*.

The *Tachycixius* species occurring in colluvial MSS from the laurel forest (*T. gomerobscurus* from La Gomera, *T. retrusus* and *T. crypticus* from Tenerife) fit with the hypogeomorphic morphotype (weakly troglomorphic, see Deharveng and Bedos 2018), while *T. lavatubus* occurring in caves of Tenerife is strongly troglomorphic. However, all the *Cixius* species (from La Palma and El Hierro), either inhabiting caves or the MSS, are highly troglomorphic. This pattern is not only true for planthoppers: many hypogean species from other groups (beetles, cockroaches, spiders) occurring in the Anaga peninsula (NE Tenerife) and La Gomera are always less troglomorphic than other congeneric species that live in more modern terrains of Tenerife, either in caves or in modern MSS (there are no recent terrains in La Gomera) (Medina and Oromí 1991; Hernández and Oromí 1993; Martín et al. 1999; Frisch and Oromí 2006).

A possible explanation is that the colluvial MSS from La Gomera and Tenerife are in old terrains covered by deep, organic rich soil inside a mature laurel forest, while in younger islands like La Palma and El Hierro any MSS is of volcanic type (Oromí et al. 1986) with less evolved soil upon and much scarcer organic matter. We hypothesize that selective pressure to evolve towards troglomorphism must be lower in rich colluvial MSS and higher in poorer volcanic MSS and lava tubes. The degree of troglomorphism does not depend on the age of the island, but on that of certain terrains within each island and their corresponding subterranean habitats.

Zoogeographic pattern and evolutionary process

In the present-day most of troglobitic planthoppers on the Canary Islands have no extant close epigean relatives, and accordingly, are relicts, i.e. „persistent remnants of formerly widespread faunas ... existing in certain isolated areas or habitats“ (Lincoln et al. 1982).

Although current knowledge does not allow to determine whether initial cave adaptation was driven by allopatry (extinction of closely related epigean populations: see *climatic relict hypothesis*, as postulated by e.g., Vandel 1964, or Barr 1968) or parapatry (by adaptive shift of troglophilic populations in order to exploit novel food resources, as suggested by Howarth 1981, see also Howarth et al. 2019), it is clear that at some point, Meenoplidae must have been represented in the epigean fauna of the Canary Islands. It is unlikely that epigean Meenoplidae are still extant, but have not yet been recorded, as the Fulgoromorpha fauna of the Canary Islands can be regarded as well known (see Bourgoin 2024: www.flow.hemiptera-databases.org, version 8, last updated 2024-01-04). Hence it is rather more likely that the cavernicolous Meenoplidae of Gran Canaria, La Palma and El Hierro, as well as the cavernicolous Cixiidae from La Gomera and El Hierro, and *partim* of Tenerife (*T. lavatubus*) are indicative of an ancient fauna which is now extinct. This is a relatively common pattern concerning many other genera of a variety of arthropod groups represented in these islands only by subterranean adapted species (Oromí 2004).

Conservation

All cave-planthopper species of the Canary Islands are single-island endemics, and known from few, in most cases a single location, and from few specimens each.

According to the IUCN Red Data Book categories they classify as *vulnerable*, due to their narrow range and specialized habitat as well as their presumed small population size. Consequently, conservation efforts need to concentrate on the preservation of areas where cave planthoppers are known to exist, on the surface as well as underground.

Major threats to the cave environment are urbanization and development which may result in the destruction of the caves proper, but also alter the surface conditions by road construction, and loss of vegetation. Deposits of sanitary and chemical waste and water pollution may be harmful for cave organisms, including planthoppers. Even more disturbing are records of increasing periods of extreme droughts which have occurred over the past several years. Consequently, the stable, saturated atmosphere which is essential

for obligate terrestrial troglobionts (Howarth 1983) is no longer maintained in the larger cave passages as it has happened in Cueva de la Curva (El Hierro), from where *Cixius ariadne*, *Meenoplus charon* and two troglobitic weevils were exclusively known but are becoming very scarce due to breakage of the end of the lava tube by loader machines working on the surface (H. López and P. Oromí, personal observation). Cave planthoppers may be able to cope with short-term adverse conditions by retreating into the smaller crevices of the MSS, which are less prone to desiccation. Long-term climate change, however, will have lasting indirect and direct influence on the subterranean environment (Howarth et al., in press). Increasing temperatures and lower precipitation will cause alteration of surface plant communities, and plant species which provide adequate roots for food supply may vanish. Sporadic observations indicate that cave planthoppers may be temperature sensitive (Hoch, personal observation on troglobitic planthoppers in Hawaii), and thus, increasing average annual temperatures may result in their extirpation.

Perspectives

Although the Canary Islands hold the highest number of cave planthopper species of any region worldwide, there are indications (observations, images, yet without voucher specimens) that more new species await discovery. It is conceivable that the number of obligate subterranean planthopper species will eventually double. Particularly promising are caves in the north of La Palma, the El Golfo region on El Hierro, as well as the extended MSS on Tenerife, Gran Canaria and La Gomera. Conversely, the eastern islands of Fuerteventura and Lanzarote are much drier, their caves lack roots inside and planthoppers have never been found there.

Troglobitic planthoppers offer unique opportunities to study adaptation to specialized habitats, including their physiology and behaviour, and their evolutionary dynamics such as subterranean speciation (Hoch and Howarth 1993; Wessel et al. 2013; Le Cesne et al. 2024). Last but not least, cave planthoppers could be models for the study of global change biology. Especially studies on their physiology to better understand physiological constraints, and long-term monitoring to assess population dynamics could contribute to a better understanding of climate change impact on subterranean environments as has been postulated by Mammola et al (2019).

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The first part of the title is borrowed from the closing statement of Charles Darwin´s book „On the origin of species by means of natural selection“ (Darwin 1859). The full text of the quotation is: *„There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning* ***endless forms*** *most beautiful and* ***most wonderful*** *have been, and are being, evolved.“*

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Supplementary material 1

Canary Islands: Distribution of hypogean planthopper species and potential epigean relatives

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